The Nutritional Ecology of Adult Female Blue Monkeys, *Cercopithecus mitis*, in the Kakamega Forest, Kenya

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ABSTRACT

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The search for food and adequate nutrition determines much of an animal's behavior, as it must ingest the macronutrients, micronutrients, and water needed for growth, reproduction and body maintenance. These macro- and micronutrients are found in varying proportions and concentrations in different foods. A generalist consumer, such as many primates, faces the challenge of choosing the right combination of foods that confers adequate and balanced nutrition. Diet selection is further complicated and constrained by antifeedants, as well as digestive morphology and physiological limitations. Nutritional ecology is the study of the connected relationships between an organism, its nutrient needs (determined by physiological state), its diet selection, and the foraging behavior it uses within a specific food environment. Additionally, these relationships are complex and changeable since the nutrient needs of a consumer change over time and food resources (including the nutritional composition) vary spatiotemporally. Published data on primate nutritional ecology are limited, with most investigations of nutritional needs stemming from captive populations and few field studies. To contribute to the body of knowledge of nutritional ecology in natural populations, I examined the nutritional ecology of wild adult female blue monkeys, *Cercopithecus mitis*. I used the geometric framework (GF) to quantify nutritional patterns, as it allows simultaneous examination of multiple nutrients that may be driving foraging behavior and patterns of food intake.

Blue monkeys are known to be generalist feeders, with flexible feeding behavior. The population I studied inhabits the Kakamega Forest, western Kenya. This forest has a history of

variable human modification on a small scale, and offered a unique opportunity to examine environmental factors (e.g. degree of human-modification of forest type, food availability), social factors (dominance rank), and physiological factors (reproductive demand) that may alter blue monkey nutritional strategies.

From January and September 2015, a team of field assistants and I collected behavioral data from 3 study groups, intensively sampling 24 adult females that varied in dominance rank and reproductive condition. I used all-day focal follows to quantify feeding behavior, which allowed me to assess diet selection and nutrient intake on a daily basis. I also monitored subjects' daily movement. To assess food availability, I quantified vegetative differences among major habitat types within each group's home range and monitored biweekly changes in plant production of fruits and young leaves, which were major constituents of the plant-based diet. I collected >300 food samples, as well as fecal samples, and analyzed them for macro-nutritional content using wet chemistry and near-infrared spectroscopy techniques. I combined data to examine patterns in diet and nutritional strategy on different scales: patterns across subjects, between groups and within the population as a whole, patterns in the diet on the food composition level versus nutrient intake level, and patterns in nutrient intake on a daily basis versus a long term basis (i.e. over the course of the study period). Additionally, I evaluated factors that might affect variation in nutritional strategies, including a female's reproductive condition, dominance rank, habitat use, and degree of frugivory or folivory in daily intake, as well as food availability in the environment.

Kakamega blue monkeys ate a broad diet of over 445 food items (species-specific plant parts and insect morphotypes). Fruit was preferred food, and particular species-specific fruits constituted the majority of important food items (i.e., those contributing >1% of total caloric

intake by group); many fruits were highly selected (i.e. eaten more than expected based on availability). Many species-specific young leaves also were important food items, though they were eaten in proportion to their availability, or even less often. Regardless of whether group diet was characterized by time spent feeding or by calories, fruit remained the largest constituent and young leaves the second largest. A subject's daily path length was negatively related to proportion of fruit in the diet (by kcal) because females focused feeding in particular trees when important fruits ripened and thus traveled less. Daily path length was not related to group size, probably because females spread out when foraging to avoid within-group scramble competition over food. Group differences in the food composition of diets likely reflected habitat differences in food distribution. Comparison of the population's diet to data from previous studies showed that as study groups moved into new areas and habitats, they capitalized on new food resources, reinforcing the idea that blue monkey are flexible feeders. During this study, subjects adjusted their diet in response to food availability in the environment, consuming more fruit (by percentage of diet and absolute kcal) when fruit was more available. In contrast, subjects ate fewer young leaves (by absolute kcal) when either fruit or young leaves were more available, suggesting that young leaves served as fallback food. At the level of nutrient intake, it was also true that females consumed significantly more structural carbohydrates when fruit availability was low. Despite their diverse diets and changes related to food availability, females actively regulated food intake to converge daily on a similar nutrient intake (grand mean of 637 kcal, with 108 kcal from protein, 149 kcal from lipid, 88 kcal from structural carbohydrates, and 293 kcal from non-structural carbohydrates, N=24). Thus, considering a multidimensional nutritional niche, I characterized their feeding behavior at two levels: they were both food composition generalists and nutrient intake specialists.

Blue monkeys showed a nutritional strategy on two different temporal scales: 1) daily protein prioritization and 2) long term non-protein energy (NPE; i.e. lipid + carbohydrate energy) to available protein (P) balancing. On a daily basis, protein intake (by kcal) showed the least amount of variation (by coefficient of variation) and subjects consumed similar amounts of protein, regardless of potential influences from environmental, social or physiological factors. Females allowed more variation in daily ratio of non-protein energy to protein (NPE:P), taking advantage of high NPE foods like fruit. They allowed higher NPE:P ratios when fruit was a larger proportion of their diet and when they spent less time in near-natural forest. There was no evidence that reproductive demand or dominance rank affected protein intake or NPE:P balance. Dominance rank also did not predict deviation (absolute or directional) from mean protein intake or mean NPE:P ratio. On a long term basis (i.e. over the 8 months of data collection), all subjects tightly balanced cumulative NPE:P intake, regardless of dominance rank. This long-term pattern in all 24 subjects suggests that it a species-typical strategy. However, lower ranking females ate more unique food items per day than higher ranking females. Varying daily dietary breadth may allow females to cope with social constraints while feeding, such that dominance rank had no effect on nutritional strategies. Further, the prevalence of NPE:P balancing in most nutritional ecology studies of primates suggests that the diversity of feeding strategies within this order of mammals may have evolved to allow them to adhere to that particular nutrient balance, though the rule of compromise (e.g. protein versus NPE prioritization) and the exact ratio balanced may differ by population or species.

Blue monkeys regularly used human-modified habitats and ate considerable amounts of the non-natural foods found there (and elsewhere in the forest). Non-natural foods were directly derived from humans or human activity (e.g. via scavenging from trash) and exotic (non-native)

plants, generally introduced inadvertently or for silviculture. Subjects incorporated a substantial amount of non-natural foods into their diets, with approximately a third of their daily calories derived from non-natural foods. Subjects in the group with the most access to human-modified habitat used non-natural foods the most extensively. Further, subjects in two groups showed clear preference for human-modified habitat while members of the third group used habitat types in proportion to their occurrence in the home range. Human-modified habitat, and the non-natural foods found within, may have been readily used because many non-natural foods provided similar access to nutritional space as natural foods. Some non-natural foods, like oil palm fruit and *ugali* (cooked maize flour), represented energetically dense food resources, which also proved attractive. Regardless of whether subjects fed primarily on natural or non-natural foods, they consumed similar amounts of daily protein. This prioritization of protein, coupled with the fact that females had higher NPE:P ratios when feeding mostly on non-natural foods, indicated that blue monkeys capitalized on non-natural resources to increase NPE intake as long as they were able to consume a threshold amount of protein. What remains unclear though, is whether there are adaptive advantages associated with the ability to consume diets of variable NPE:P ratios.

Overall, blue monkeys in Kakamega Forest are very flexible feeders, perhaps to a greater degree than previously acknowledged. Subjects were able to consume a diverse diet of hundreds of species-specific food items, to shift their diet in response to changes in food availability, to capitalize on food resources found in different habitat types, to take advantage of non-natural food resources, and to tolerate a wide range of NPE:P ratios in daily diets. Further, on a nutritional level, they successfully navigated potential stressors from the physiological demands of reproduction and dominance rank to adhere to a particular nutritional strategy. Flexible

behavior, such as spreading out during feeding or varying dietary breadth, indicates how blue monkeys may use particular feeding strategies to arrive at a common nutrient intake target. Despite daily fluctuations in NPE:P ratio that varied with environmental and dietary factors, all subjects were able to consume a consistent daily amount of protein and prioritized its intake above all other nutritional components. Finally, their tight adherence to long term NPE:P balancing suggested that they followed a nutritional strategy that operated on both daily and longer timescales.

Primates are increasingly threatened from habitat loss, degradation and other human-disturbances. There is growing awareness that some species, like blue monkeys, may be able to persist in regenerating human-modified landscapes, where they regularly and readily use non-natural food resources. More species- and habitat-specific nutritional studies are needed to predict population-level responses to varying degrees of habitat alteration. The data generated may help us assess the potential value of human-modified habitats that may require protection, as these habitats may contribute to the persistence of primate populations around the globe, especially in novel ecosystems.

TABLE OF CONTENTS

FIGURES AND TABLES ii

ACKNOWLEDGEMENTS iv

DEDICATION viii

CHAPTER 1: INTRODUCTION 1

CHAPTER 2. CHARACTERIZING THE NUTRITIONAL ECOLOGY OF ADULT FEMALE BLUE MONKEYS IN KAKAMEGA FOREST, KENYA 23

CHAPTER 3: THE NUTRITIONAL STRATEGY OF ADULT FEMALE BLUE MONKEYS: DAILY PROTEIN PRIORITIZATION AND LONG TERM MACRONUTRIENT BALANCING 94

CHAPTER 4: THE ROLE OF NON-NATURAL FOODS IN THE NUTRITIONAL STRATEGIES OF ADULT FEMALE BLUE MONKEYS IN A HUMAN-MODIFIED MOSAIC LANDSCAPE 150

CHAPTER 5. CONCLUSION 204

REFERENCES 211

APPENDIX 236

FIGURES AND TABLES

CHAPTER 2 67
Figure 2.2. Monthly variation in rainfall at study site in Kakamega Forest, Kenya during this study 68
Figure 2.3. Variation in food availability index (FAI) for fruit 69
Table 2.1. Vegetation composition of the three habitat types 70
Table 2.2. Focal follow summary, showing time (hr) spent feeding, in and out of sight, and follow length 71
Figure 2.4. Population diet composition by item, expressed in terms of mean % feeding time (blue) and mean % calories ingested (red) across 371 female-days 72
Figure 2.5. Important foods by group 73
Figure 2.6. Shared important foods by group 75
Table 2.3. Linear mixed models for relationships between diet (% fruit (computed using kcal), absolute amount (kcal) of fruit, absolute amount (kcal) of young leaves) and food availability 76
Table 2.4. Selection ratios for fruit and young leaves of major food species 77
Figure 2.7. Relationships among diet and food availability 78
Table 2.5. Daily intake by group and population 79
Table 2.6. Significant differences in daily intake by females in different groups 80
Figure 2.8. Boxplots for daily nutrient intake differences for females in different groups 81
Table 2.7. Significant differences in daily intake by females during low versus high fruit availability periods 82
Figure 2.9. Boxplots for daily intake differences of females in periods of low versus high fruit availability 83
Figure 2.10. RMTs of individual daily diet intake means 84
Figure 2.11. RMTs of group diet menu and grand mean group daily diet intakes 85
Figure 2.12. RMT comparisons of expected diets (based on relative food availability) and observed daily diet intakes 86
Table 2.8. Grand mean daily path length (DPL) for individual females, by group and for the population 87
Table 2.9. Linear mixed model for predicting daily path length 88
Figure 2.13. Relationship between daily path length and percentage of fruit in diet 89
Figure 2.14. RMT of Kakamega blue monkey diet compared to other guenons, chimpanzees and gorillas in other East African locations 90
Table 2.10. Plant species previously found in the diet of Kakamega Forest blue monkeys 91
Figure 2.15. Longitudinal comparison of diet compositions of female Kakamega blue monkeys 92
Table 2.11. Range of percentages of food item types reported in blue monkey diets 93

CHAPTER 3 126
Table 3.1. Study groups' size (mean for all members, January 24-September 25, 2015), home range size, and habitat composition 126
Figure 3.1. Protein leverage hypothesis 127
Table 3.2. Mean and SD of variables used as fixed effects in linear mixed models that predicted NPE:P ratio and protein intake (kcal) 128
Table 3.3. Variation in daily intake of energy and nutrients 129
Figure 3.2. Variation in individuals' daily intake of protein (kcal) 130
Figure 3.3. Variation in individuals' daily intake of lipid (kcal) 131
Figure 3.4. Relationship between NPE and protein intake 132
Table 3.4. OLS regression model statistics for subjects' relationships between cumulative NPE and cumulative P 133
Figure 3.5. Cumulative NPE:P balancing for individuals in three study groups 134

Figure 3.6. Relationship between cumulative NPE and cumulative protein intake (kcal)..... 138
Figure 3.7. Protein leverage in diets of blue monkeys..... 139
Figure 3.8. Variation in individuals' daily intake of non-protein energy (kcal)..... 140
Table 3.5. Linear mixed models predicting NPE:P ratio for a) all data and b) data excluding outliers..... 141
Figure 3.9 Negative relationship between NPE:P ratio and standardized FAI ripe fruit..... 142
Figure 3.10. Positive relationship between NPE:P ratio and standardized percentage of fruit in daily diet..... 143
Figure 3.11. Negative relationship between NPE:P ratio and standardized proportion of daily time spent in near-natural forest..... 144
Table 3.6. Linear mixed model predicting protein intake..... 145
Table 3.7. Linear mixed model predicting deviation from nutritional strategy as a function of dominance rank..... 146
Figure 3.12. Negative relationship between daily unique food items and standardized rank..... 147
Table 3.8. Linear mixed model predicting NPE intake..... 148
Table 3.9. Linear mixed model predicting total energy intake..... 149

CHAPTER 4..... 182
Figure 4.1. Home range size and habitat composition, showing three study groups' differential access to multiple habitat types..... 182
Table 4.1. Vegetation composition (basal area, cm^2 per ha) in the three habitat types..... 183
Table 4.2. Non-natural foods of Kakamega blue monkeys, both exotic plant foods and human-derived..... 189
Table 4.3. Non-natural foods in the daily diet by group, showing the percentage of non-natural calories, total energy intake, and macronutrient intake..... 190
Table 4.4. Significant differences in daily intake of non-natural food by females in different groups..... 191
Figure 4.2. Boxplots for daily non-natural nutrient and energy intake differences for females in different groups..... 193
Table. 4.5. Likelihood ratio tests for testing the significance of group as fixed effect in predicting non-natural nutrient and energy intake..... 194
Table 4.6. Important non-natural food items by group, ordered left to right by the percentage of human-modified habitat in home ranges (GSC highest)..... 195
Table 4.7. Cross-group comparison of habitat representation in the home range and mean ± SD percentage of day spent in different habitat types..... 196
Table 4.8. Model (zero-inflated beta regression) for relationship between percentage of day spent in human-modified habitat and percentage of daily calories sourced from non-natural foods..... 197
Figure 4.3. Positive relationship between consumption of non-natural food and use of human-modified habitat..... 198
Table 4.9. Linear mixed model for the relationship between type of feeding day and NPE:P ratio or protein intake..... 199
Figure 4.4. Daily NPE:P balancing when feeding on mostly natural versus non-natural foods..... 200
Figure 4.5. Protein intake when feeding on mostly natural vs. non-natural foods..... 201
Figure 4.6. RMT of natural versus non-natural food nutritional spaces, demonstrating the nutritional space for natural and non-natural foods..... 202

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DEDICATION

I dedicate this thesis to my parents Reid and Wendy Takahashi,

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They give me courage to chase my dreams.

CHAPTER 1: INTRODUCTION

The process of obtaining food relates to all aspects of a species' natural history, from behavior, to cognition, to morphological adaptation [Robbins, 1993; McNab, 2002]. Placing that process in the context of a specific habitat is key to understanding the behavioral choices an animal makes regarding food and the consequences those choices have on its lifetime reproductive success. Further, adequacy and quality of food directly influence the viability of populations. Individuals make the daily effort to not only meet their physiological maintenance needs, but also to acquire extra food for reproductive efforts [Krebs & Davies, 1997]. Adequacy of food refers to the ability of available food to provide enough nutrition and energy to meet an animal's maintenance and reproductive needs, usually measured by the change in a dependent factor such as body mass [National Research Council, 2003]. The quality of food refers to the amount of nutrients and energy in a food and is determined by an animal's physiological ability to extract the nutrients and energy while at the same time avoiding antifeedants such as overly high levels of indigestible or harmful components (e.g. lignin or toxins; [Oftedal, 1991; National Research Council, 2003; Lambert, 2007]). As a result, researchers are interested in understanding how much (adequacy) and what types (quality) of food an animal requires, and how those needs are met in particular environmental contexts.

Here, I present research results on the feeding ecology of a population of blue monkeys, *Cercopithecus mitis*, in the context of its environment in Kakamega Forest, Kenya. The thesis is divided into five chapters. This introductory chapter has three aims. First, it provides the reader with a brief introduction to primate nutrition, in terms of energy, macronutrients, micronutrients, water, and antifeedants. Second it describes digestive physiology in primates. Third, it introduces

nutritional ecology with a discussion of Geometric Framework, a recent and promising analytical method to identify single or multiple parameters driving nutrient intake [Simpson & Raubenheimer, 2012].

The second chapter examines variation in the diets of adult female blue monkeys with three aims: First, I describe the diet, identifying important foods and evaluating their consumption in relation to their availability. Second, I evaluate the diet in terms of the multidimensional nutritional niche, a multi-level approach to understanding dietary variation using both food type and nutrient intake levels. Third, I explore one consequence of variation in diet, namely its effect on daily path length. I conclude with a discussion of the dietary variation observed in this study compared to previous studies of the same population, as well as other populations and guenons in general.

The third chapter focuses on feeding and nutritional strategies of individuals, specifically how they regulate food intake to consume adequate nutrients, and on the patterns in nutrient consumption observed across daily food intakes. The first aim was to characterize the patterns of nutrient consumption using the Geometric Framework, a new method in nutritional ecology, to examine whether subjects consumed a balanced ratio of particular nutrients or prioritized consumption of one nutrient. The second aim was to examine factors that influence nutritional strategies, particularly social dominance, differential patterns of habitat use, and reproductive demand. I discuss this study's results in the context of other nutritional ecology studies of primates.

The fourth chapter focuses on the role of human-modified habitat and non-natural food resources in the nutritional ecology of blue monkeys in the Kakamega Forest. I first describe the prevalence and use of non-natural food (human-derived food and food from exotic (non-native)

plant species). Second, I explore whether use of human-modified habitat relates to consumption of non-natural food. Third, I explore how non-natural foods in the diet affected nutritional strategies. I also discuss the value of human-modified habitat and non-natural foods to conservation and population management strategies.

The final and fifth chapter is the conclusion. I review the major findings from my dissertation study and their implications.

COMPONENTS OF NUTRITION

What is meant by the term nutrition? "Nutrition is the process whereby the animal procures and processes portions of its external chemical environment for the continued functioning of internal metabolism" [Robbins, 1993, p.6]. The specific components of the external environment that constitute nutritional requirements are carbohydrates, amino acids from protein, essential fatty acids from fat, water, minerals, and vitamins [Robbins, 1993]. Of these requirements, carbohydrates, protein, and fat collectively form macronutrients, components needed in large quantities and that provide energy to the animal [Robbins, 1993].

Energy is not a nutrient in the chemical sense, but is an abstraction to measure the amount of fuel that an animal consumes from food [National Research Council, 2003]. Common units of energy are calories or joules. Gross energy (GE) is the total amount of energy released from an organic compound as it is oxidized to carbon dioxide and water [National Research Council, 2003]. However, not all this energy is available to the consumer since certain parts of the food may be indigestible and the digestive process is not entirely efficient [Robbins, 1993]. A more accurate measure of energy obtained from food is metabolizable energy (ME), which is the GE of the diet subtracted by the GE of the feces (thus accounting for digestibility of food) and

subtracted by the energy loss to urine and gas production [National Research Council, 2003]. ME is a better measurement than GE of energy available to the animal.

A critical component of ME is protein, and more specifically the amino acids it provides, as protein is important for processes such as building cell walls and sustaining enzymatic activity [Robbins, 1993]. Animals are able to produce some, but not all, amino acids. The amino acids that must be obtained from the external environment via food consumption are considered *essential* amino acids [Robbins, 1993]. To obtain these amino acids, animals must consume some portion of their diet as protein. There are two types of protein: *complete* and *incomplete*. A *complete* protein source provides all essential amino acids, though the number and identity of essential amino acids differ by species of consumer. *Incomplete* proteins provide only some of the essential amino acids and these proteins must be consumed in complementary combinations. Most wild primates are able to fulfill most of their daily protein requirements from plants. Protein is commonly obtainable from seeds, and young and mature leaves, and flowers [Milton, 1979, 1999, 2008; Lambert, 1998a; Norconk et al., 2009]. If primates are able to digest leaf material, plants are an excellent source of protein, with young leaves generally higher in protein than mature leaves [Milton, 1999]. Animal prey (both insects and vertebrates) is also a rich source of protein, especially essential amino acids, though often more difficult or unpredictable to obtain than plants [Lambert, 1998b; Bryer et al., 2013; Raubenheimer & Rothman, 2013; Lambert & Rothman, 2015]. Young infant primates require relatively large amounts of protein, and the protein in milk supplies infants with 7-22% of their energy. Adult primates most likely require 5-8% of their ME as protein, though pregnant or lactating females may require more [12.5%; Oftedal, 1991].

Another component of energy is fat, which provides fatty acids, with some termed *essential* fatty acids because they are available to an animal only via ingestion from the external environment [Robbins, 1993]. Essential fatty acids cannot be produced by the animal from any precursor and for primates, they include the n-3 and n-6 fatty acids [National Research Council, 2003]. Fatty acids are important components of cell membranes and are necessary to produce the metabolites that regulate cellular activity. The necessary amount of essential fatty acids of the total caloric intake is only 1-2%, but this may vary by age. Younger primates may need more essential fatty acids because of growth and elevated metabolism. Essential fatty acids can also be stored in the body, so older individuals can access their reserve and the need for active ingestion of essential fatty acids declines with age. Fat is most easily obtained from seeds, animal prey, and some fruit [Lambert, 1998b; Milton, 1999, 2008; Norconk et al., 2009; Lambert & Rothman, 2015]. Fat is the most energy-dense macronutrient.

Carbohydrates, the last of the three macronutrients, comprise several types of carbon-based molecules (e.g. mono-, di-, oligo- or polysaccharides) and chains of smaller molecules. Carbohydrates are classified in various ways, all reflecting the fact that these molecules contain energy in forms that are the easiest and most difficult to convert. One such classification, based on molecular size, distinguishes *simple* versus *complex* carbohydrates. Simple carbohydrates are widely available in foods with a high sugar content, such as the pulp of ripe fruit [Lambert, 1998a]. Simple carbohydrates are readily converted into usable energy whereas complex carbohydrates require extensive processing. Another classification, based primarily on the function of these compounds in plant tissue, distinguishes *structural* versus *non-structural* carbohydrates [National Research Council, 2003]. Of the non-structural carbohydrates (TNC), monosaccharides and disaccharides are considered soluble sugars. Polysaccharides are complex

polymers of monosaccharides and are either starch-like or non-starch. Starch-like compounds are readily digestible by primates, but non-starch polysaccharides are either soluble or insoluble. Soluble non-starch polysaccharides are referred to as soluble fiber and are nonstructural polysaccharides. These can be digested via fermentation, though not as completely as starch-like compounds. Gums are a form of soluble non-starch polysaccharides. Structural carbohydrates, by contrast, refer to the insoluble non-starch polysaccharides, cellulose and hemicellulose, and are commonly referred to as insoluble fiber. Some primates have evolved a compartmentalized gastric system that facilitates fermentation of cellulose, hemicellulose, and soluble fiber. Symbiotic gastrointestinal anaerobes break down these carbohydrates and release energy usable to the host.

Carbohydrates provide upwards of 40% of ME in the diets of many primates and are the most abundant compound in plants [National Research Council, 2003]. For example, total carbohydrate comprises 55-59% of the nutritional value of plant foods eaten by western gorillas, *Gorilla gorilla gorilla*, [Calvert, 1985], and 57-65% in plant foods eaten by Ugandan forest primates [Conklin-Brittain et al., 1998]. Carbohydrates are of considerable interest to primate nutritional ecologists because some species have evolved physiological and behavioral adaptations to deal with digesting structural carbohydrates (see below section on physiological adaptations). By definition, structural carbohydrates are more prevalent in the fibrous parts of the plant: stems and mature leaves. Younger parts of the plant (e.g. young leaves and stem tips) contain a lower concentration of structural carbohydrates [Milton, 1979]. Non-structural carbohydrates, by contrast, are found in the highest concentrations in fruits, flowers, and some plant exudates. Seeds and underground storage organs are high in digestible starch [Lambert, 1998b; Milton, 1999, 2008; Norconk et al., 2009].

Unlike macronutrients, micronutrients do not provide energy and are needed in only small quantities, but they are nonetheless necessary for the normal functioning of physiological processes [Lambert, 2007]. Micronutrients comprise two classes, minerals and vitamins. Minerals are diverse inorganic molecules, and most information about mineral requirements derives from studies of domestic and laboratory animals. Requirements for such animals are probably significantly different from those of wild counterparts [Robbins, 1993]. Mineral requirements, similar to macronutrient requirements, are determined by factors such as age and reproductive condition [National Research Council, 2003]. Primates obtain most of their required minerals from plant tissues (including rotting wood and pith; [Struhsaker et al., 1997; National Research Council, 2003; Rothman et al., 2006; Cancelliere et al., 2014]), animal tissues, especially insects [Milton, 2003; Raubenheimer & Rothman, 2013], and less commonly, dirt [National Research Council, 2003]. While it is generally thought that wild primates have adequate access to minerals, some populations may be mineral-limited: for example, redtail monkey, *Cercopithecus ascanicus*, densities in different areas of Kibale National Park, Uganda correlate with copper content in the diets [Rode et al., 2006].

Vitamins are organic micronutrients. Most vitamins must be ingested as a component of food, though some can be obtained by bacterial synthesis in the gastrointestinal tract. Vitamins are classified into two groups: water-soluble and fat-soluble. Fat-soluble vitamins are absorbed along with fat into the body via the intestinal tract and can be stored in fat tissues and liver, where they are sources for the body to draw upon in case of vitamin shortages in ingested food. Excessive storage of vitamins can, however, be toxic. Unlike fat-soluble vitamins, most water-soluble vitamins cannot be stored by the body and must be consumed on a regular basis

[Robbins, 1993]. Vitamins are found in a variety of foods, especially fruits, seeds, and leaves [Lambert, 1998b].

Of all nutrients, water is one of the most important essential nutrients because it composes 99% of all molecules within an animal's body. Animals obtain water in various ways: they may ingest free water from external sources such as streams or dew, water that is part of ripe fruit and fleshy leaves [Lambert, 1998b], and oxidative or metabolic water produced by the oxidation of organic compounds containing hydrogen [Robbins, 1993; National Research Council, 2003]. Obtaining water is a challenge for only a few species of primate, particularly those whose habitats experience extreme droughts (e.g. *Papio sp.* in arid regions [Altmann, 1974]).

Understanding primate nutrition not only requires knowing what nutrients and foods are sought, but also knowing which components of food are avoided or minimized. Antifeedants are the chemicals in a plant that deter consumers from feeding, usually by slowing the consumption rate or by interfering with nutrient digestion [Lambert, 2007]. Antifeedants directly reduce the food's quality by imposing direct costs on consumers (versus indirect food costs like search time). There are two types of antifeedants generally distinguished in the primate nutrition literature: fiber and secondary metabolites.

Fiber, as discussed above, is a general term referring to both soluble and insoluble fiber, as well as non-carbohydrate components of the cell wall like lignin, cutin, and waxes. Since primates can digest only a portion of dietary fiber, the fiber content in the diet acts like a dilutant, affecting nutrient density of food [Lambert, 2007]. Also, fiber digestion through fermentation requires a relatively long time, and this lengthy digestion limits the rate at which primates can consume and process food.

Secondary metabolites in plants serve to protect the plants against herbivory. These organic substances are stored in plant tissues and often confer a bitter taste or an offensive odor to humans [Lambert, 2007]. There are two main categories: digestion inhibitors and toxins [Lambert, 2015]. Tannins are digestion inhibitors that bind to proteins and interfere with protein absorption [Wallis et al., 2012]. By contrast, toxins directly and negatively affect an animal's physiology. Primates regulate, and to a certain extent, tolerate, secondary metabolites in the diet [Wrangham & Waterman, 1981, 1983; Norconk & Conklin-Brittain, 2004; Eppley et al., 2017]. Some strategies to cope with them include geophagy, charcoal consumption, or long gut retention times for microbial detoxification [Struhsaker et al., 1997].

Primates must meet simultaneous demands of energy, macronutrients (protein, lipid, and carbohydrates), and micronutrients, while also avoiding antifeedants. The National Research Council (NRC; [2003]) suggested specific dietary guidelines for non-human primates by generalizing data from a few model taxa across the order Primates. They proposed that primates (post-weaned) fed purified or semi-purified foods required diets with nutrient concentrations of 3% lipid, 8-18% crude protein, and 10-30% structural carbohydrate (as measured by neutral detergent fiber (NDF) assay; all percentages on a dry matter basis; see [National Research Council, 2003] for micronutrient estimates). The recommended diets assume high bioavailability of nutrients and no adverse interaction among nutrients.

Because of the intensive field and laboratory effort required in measuring nutrient intake, limited data are available for wild primates. Conklin-Brittain et al. [1998] reported monthly mean nutritional composition of diets, weighted by time spent feeding on different foods, for four primates in Uganda: chimpanzee (*Pan troglodytes schweinfurthi*), gray-cheeked mangabey (*Lophocebus albigena johnstoni*), red-tailed monkey (*Cercopithecus ascanius schmidti*), and

blue monkey (*Cercopithecus mitis stuhlmanni*). All four species' diets ranged within 3-4% lipid, 10-18% crude protein, and 31-34% NDF. Using a similar method, Norconk and Conklin-Brittain [2004] reported that the diet of Venezuelan white-faced sakis (*Pithecia pithecia*) was 16% lipid, 7% crude protein, and 38% NDF. The Catarrhine primate values agree with the range proposed by the NRC, and the saki values are close. One other study, however, reported very high lipid values: the diet of aye-ayes (*Daubentonia madagascariensis*) was 42-55% lipid, 6-15% available protein and 32-50% NDF [Sterling et al., 1994]. This population spent >90% of feeding time on four foods, three of which were high in lipid (33-60% lipid, on a dry matter basis). Perhaps aye-ayes use lipids, rather than carbohydrates, as their primary energy source.

The composition of a primate's diet determines the concentrations of different nutrients. For example, fruits generally are high in non-structural carbohydrates and variable in lipid, leaves generally are high in protein but also high in fiber, and animal matter is high in protein and may be high in lipid. Since food types differ in nutritional composition and to effectively use certain types of food, species evolved different digestive morphologies and strategies. The next section discusses how a primate's gastrointestinal design and function is closely related to the type of diet it consumes.

FACTORS DRIVING DIETARY VARIATION IN PRIMATES

A primate's digestive physiology influences its dietary decisions [Chivers & Hladik, 1980; Lambert, 1998b; McNab, 2002]. Primates display a wide range of digestive adaptations and these both enable and prevent exploitation of particular food resources. Every primate possesses the necessary anatomical and physiological traits to exploit its particular feeding niche, such as thick tooth enamel to consume tough bark [Lambert et al., 2004], a modified finger for

insect predation [Sterling, 1994], or specialized stomachs to ferment high-fiber foliage [Lambert, 1998b]. These traits allow primates to exploit a wide spectrum of diets and possible foods.

The morphology of the digestive tract determines a primate's ability to process its diet. Lambert [1998 a] provides an overview of the primate gastrointestinal tract and its major regions: stomach, small intestine, and large intestine comprising caecum and colon (caeco-colic region). Protein digestion occurs primarily in the stomach while lipid digestion occurs primarily in the small intestine. Carbohydrates vary in digestion location, with the two main sites being stomach and intestines. Primate stomachs can be a single chamber or multi chambered: the latter enables the tract to vary the retention time of food in an acidic environment [National Research Council, 2003]. Additionally, the walls of the digestive tract may be either simple or contain folds (i.e. haustrations), which affect the passage rate of food material and the amount of time available to gut microbia to digest the food [Chivers & Hladik, 1980]. Folds also increase the amount of surface area of the gut that contacts food material, which enhances nutrient absorption. Primates may have pregastric digestive compartments that digest food via fermentation by endogenous enzymes. In primates without pregastric compartments, carbohydrates can be digested in the hindgut via fermentation by microbes [National Research Council, 2003]. The size of the gut and its adaptations are offset by the energy requirements needed to support such an extensive system.

Since food types (e.g. leaves versus fruits) vary in nutritional composition, there is a general relationship between the type of gastrointestinal tract a primate has and the type of diet it consumes [Lambert, 1998b]. Primates relying mostly on animal matter have relatively simple, unspecialized digestive tracts since invertebrates and small vertebrates are nutritiously dense [Chivers & Hladik, 1980; National Research Council, 2003; Rothman et al., 2014; Lambert &

Rothman, 2015]. Because the small intestine is the major site of nutrient absorption for faunivores, their ratio of stomach and ceaco-colon region to small intestine (by area, weight, and volume) is relatively low compared to frugivorous or folivorous primates [Chivers & Hladik, 1980; Lambert, 1998b; National Research Council, 2003]. While animal prey may be easily digestible food, the exoskeletons of certain species of invertebrates are not. Exoskeletons contain chitin, a type of structural carbohydrate. Many insectivorous primates, such as tarsiers, break down chitin in the cecum using microbial fermentation [Lambert, 1998b].

The gastrointestinal tract of frugivores is specialized to an intermediate degree and the ratio of stomach and large intestine to small intestine is intermediate between faunivorous and folivorous primates [Chivers & Hladik, 1980]. Specialization occurs in species that rely more on leaves, rather than animal matter, to supplement their protein-poor fruit diet [Lambert, 1998b]. These primates generally have complex caeca that facilitate bacterial fermentation [National Research Council, 2003]. In addition, the intestine and colon may be haustrated or elongated, to increase the absorption of nutrients.

The gastrointestinal tract of folivores is the most specialized and has the highest ratio of stomach and small intestine to large intestine compared to the other dietary categories [Chivers & Hladik, 1980]. Folivores must solve the problem of digesting the cell wall of leaves and other plant tissues, which comprise structural, complex components like cellulose, hemicellulose, lignin, and pectin [Lambert, 1998b]. These structural carbohydrates are found only in plants, and are difficult for vertebrates to digest. The only enzyme used for digesting cellulose, cellulase, occurs only in some invertebrates: no known vertebrate produces this enzyme. As a solution, and as noted above, vertebrates host symbiotic microorganisms in their digestive tract to digest these carbohydrates [Chivers & Hladik, 1980]. The microbes break down the carbohydrates during

fermentation and release volatile fatty acids, which the host uses as a source of energy. The microorganisms themselves are also useful because when they die, the host animal's digestive enzymes extract protein from them.

Morphological features of the gastrointestinal tracts also facilitate fermentation for folivorous primates. These animals have either a large, sacculated stomach or an enlarged caeco-colic region for fermentation [Milton, 1979; Chivers & Hladik, 1980; Lambert, 1998b]. Fermentation requires a longer retention time of ingesta, allowing the animal more time to absorb nutrients. Colobines are the only primates with a forestomach specialization: their modified stomach includes multiple chambers with different pH levels that optimize microbial activity or different microbe communities. The need to keep two different levels of pH in the stomach influences a colobine's feeding habits. The consumption of ripe fruits must be regulated as the flesh can decrease forestomach pH, which can be harmful (i.e. acidosis). For primates that use caeco-colic fermentation, additional microbial fermentation occurs after the ingesta has passed through gastric and enzymatic digestion. The intestines are generally elongated and haustrated to slow the movement of the ingesta, allowing more complete fermentation and absorption of nutrients. Caeco-colic fermentation is the most efficient system when the diet comprises foods that contain relatively digestible components, while forestomach fermentation is more efficient when the diet comprises foods that are high in structural carbohydrates.

The retention time, or the rate at which digesta move through the gastrointestinal tract, is also an important feeding adaptation as it relates to an animal's ability to absorb and process nutrients [Chivers & Hladik, 1980; Lambert, 1998b]. Digestive absorption is the ability of the tract to assimilate important nutrients, both macro and micro, into the body while processing refers to the ability to pass digesta through the tract at a rate sufficient to acquire enough

nutrients to satisfy energy and nutrient requirements. Generally, there is an inverse relationship between the length of time the food travels through the tract and the total amount of food that can be processed at a given time. Primates with slow rates of passage (long retention time) emphasize nutrient absorption and rely on relatively small amounts of high-fiber food such as leaves, which take a long time to digest. Primates with fast rates of passage (short retention time) emphasize processing and rely on large amounts of foods with easily digestible nutrients and readily available energy from simple carbohydrates, such as fruit [Lambert, 1998b]. However, compared to other mammalian groups, the relationship between body size and retention time is fairly weak [Lambert, 1998b]. Small bodied callitrichines and galagines follow the trend, as do large bodied hominoids. However, mid-sized primates show a wide range of retention times in relation to body mass, indicating the general flexibility that primates as a whole show in physiological adaptations in relation to diet.

There are other factors besides digestive physiology that influence variation in primate diets. An important one is metabolic rate. Kleiber's Law specifies how body size relates to basal metabolic rate: because of allometric scaling effects, this relationship is non-linear. As body size decreases, the basal metabolic rate per unit of body mass increases disproportionally [Kleiber, 1932]. Thus, smaller animals must consume more nutrients per unit body mass than larger animals. Smaller animals are also limited by gut capacity, however, so to consume the minimum amount of nutrients they need, smaller animals selectively forage for food that is more dense in nutrients [Temerin et al., 1984]. This interaction between body size, nutritional needs, and diet selection can be conceptualized with Kay's threshold [Kay, 1973, 1984], which explains dietary patterns among primates based on body size. Large primates have the digestive capacity to subsist on large quantities of fibrous leaves. Kay's threshold describes the point at which smaller

primates switch to including insects as part of their diet to meet their nutrient demands. Since insects are heterogeneously distributed over a landscape, the encounter rate of insect prey remains constant regardless of body size. Therefore, only small primates will be able to encounter and consume enough insects to meet nutritional demands [Milton, 2006]. This size threshold tends to occur around 500 g of body mass, below which primates must include insects as part of their diet [McGrew, 2001]. They may also supplement their diet with other items such as other animal matter, exudate, or fruits [McGrew, 2001]. Marmosets (genus *Callithrix*) and slow lorises (genus *Nyticebus*), which are small-bodied, are an exception to the rule as they consume large amounts of gum, which is considered poor quality food because it is high in complex carbohydrates [Lambert, 1998b; Cabana et al., 2017]. Longer retention times in the animals allow for slower digestion and gum is even selectively retained and fermented in the caecum, while other foods pass more quickly through the intestine [Lambert, 1998b].

In summary, animals strive to consume high quality foods, where high quality is contingent upon an animal's ability to digest a food resource. A primate's digestive tract is a reflection of the diet it consumes, with specific adaptations aimed at efficiently digesting a diet category: animal matter, leaves, fruits, or a combination of those three. The varied gastrointestinal adaptations reveal how primates are able to display the full range of diet patterns, while metabolic demands constrain which foods are acceptable. The next section will discuss how diet patterns relate to nutrition and to the environment.

IMPORTANCE OF NUTRITIONAL ECOLOGY

Early research on how diet related to the environment used optimal foraging theory, which emphasized efficiency, based on either energy maximization or time minimization, and

paved the way for regarding feeding behavior and diet selection as evolved strategies for consuming nutrients [Emlen, 1966; MacArthur & Pianka, 1966; Pyke et al., 1977]. Energy, however, is just one of the many properties of food that determines an animal's foraging decisions. Recent research has emphasized that the nutritional quantity and composition of food critically influences how an animal selects food from the environment [Simpson et al., 2004; Simpson & Raubenheimer, 2012] . Nutritional ecology is the study of the interaction between an organism and its environment, in regards to how it navigates the nutritional, spatial, and temporal heterogeneity of its surroundings to acquire food, taking into account its physiological state [Milton, 2006; Raubenheimer et al., 2009].

Much of what we know about nutritional ecology of primates originates from studies that examined gut morphology in relation to fiber digestion in ruminants, emphasizing the complex relationship between an animal's nutritive needs, its food environment, and its digestive capacity to use available foods [Van Soest, 1994]. Foods found in the environment are basically packages of nutrients and not all packages are equal, so food items (species-specific plant parts, fungi, or animals) need to be assessed for their nutrient composition. Species of plant differ in their nutritional value and even within a species, the nutritional value of its parts can vary over a temporal and spatial scale [Ganzhorn, 1995; Conklin-Brittain et al., 1998; Chapman & Chapman, 2002; Chapman et al., 2003; Worman & Chapman, 2005; Houle et al., 2007; Rothman et al., 2009, 2012; Lambert & Rothman, 2015]. The variation in nutritional values, and the fact that there may be constraints on diet selection (e.g. tannin content or fiber indigestibility) means that primates will tailor their diet selection based on their food environment, thus controlling, as much as possible, nutrient intake [Wasserman & Chapman, 2003]. Indeed, research has shown that selected foods are higher in nutritional content than nonfood/unselected items (e.g.

[Hohmann et al., 2010; Johnson et al., 2012]). Diet selectivity and the existence of digestive adaptations means that the nutritional quality of the habitat may not necessarily reflect the quality of the consumer's diet. Also, variation in nutritional composition of plant food items along a spatiotemporal scale suggests that though diets may be composed of similar items, they may actually confer different nutrient intakes; and vice versa, it is possible that diets composed of different items nevertheless converge in terms of nutrient intake (see Chap 2).

A major goal of nutritional ecology is to assess the optimal amount and balance of nutrients required by an animal per unit time in a given environment. A recent model for studying nutritional ecology is the geometric framework (GF, [Raubenheimer et al., 2009]). The GF allows one to assess all potentially relevant nutritional (micro or macro) or non-nutritional (anti-feedants, energy) parameters that guide an animal's feeding decisions, without making *a priori* assumptions about which of them are most critical [Felton et al., 2009a; Raubenheimer et al., 2009]. The GF provides a more comprehensive analysis of diet than classic optimal foraging theory because it is not a single factor model (i.e. focusing on only energy or time as a dietary determinant), and can instead simultaneously test multiple parameters. As an animal forages and consumes food, it is also navigating a multidimensional *nutritional space,* determined by the nutrients in the available foods in its environment [Simpson & Raubenheimer, 1995].

Studies using the GF have shown that achieving a balanced ratio of nutrients underlies the foraging behavior of many species, from slime molds to large vertebrates, even when one or more nutrient(s) is limiting in the environment [Simpson & Raubenheimer, 1995; Raubenheimer & Simpson, 1997; Dussutour et al., 2010; Erlenbach et al., 2014; Remonti et al., 2016]. *Nutrient balance* can be visualized as a line through nutrient space, with each axis representing a critical nutrient. Over a given period (e.g. a day), there is a point on this line that represents the nutrient

intake target, which is the amount and balance of nutrients needed for optimal performance and accounting for any inefficiencies in digestion [Simpson & Raubenheimer, 2012].

There are two ways to identify nutrient intake targets [Simpson & Raubenheimer, 1995]. The first is to use measures of performance that represent fitness. The performance measure (e.g. growth rate for juveniles or reproductive success for adults) is plotted against proportions of nutrients, for example two macronutrients, and the highest point on the 3-dimensional surface is the nutrient target. The second method to identify nutrient targets is to use evidence from mechanisms. A researcher may observe a certain point in the nutrient space, the intake target, that an animal "defends" or adheres to with relatively little fluctuation, regardless of variable nutritional environments [Raubenheimer & Simpson, 1997]. This target can be observed in both field and lab environments. An animal may change diet selection or consumption to defend this target in nutrient space. For example, when locust nymphs, *Locusta migratoria*, were given four foods of varying protein and carbohydrate ratios, all treatment groups converged on the same intake target in nutrient space by consuming various volumes of the food [Raubenheimer & Simpson, 1997]. Lab work indicates that chickens, rats, and insects all adhere to a target in nutrient space when given foods of various nutritional compositions [Raubenheimer & Simpson, 1997].

An absence of intake target defense indicates that the available foods do not provide an animal with the optimal balance of nutrients, and an animal is forced to *prioritize* one or more critical nutrients. In so doing, it may allow the ingestion of one or more less critical nutrients to fluctuate from an optimal amount. These deviations characterize the animal's *rules of compromise*. For example, when lab rats (*Rattus sp.*) were fed treatment diets that did not allow them to reach their intake targets, they prioritized eating protein to the target level, but

disregarded the amount of carbohydrates consumed [Simpson & Raubenheimer, 1997]. Similarly, wild spider monkeys (*Ateles chamek*) in Bolivia prioritized protein intake and allowed total energy intake to vary [Felton et al., 2009b]. In contrast to protein prioritization, wild gorillas (*Gorilla beringei*) in Uganda prioritized non-protein energy (NPE; i.e. fat+carbohydrate energy) and ate surplus protein to meet their energetic demands [Rothman et al., 2011]. Similar to gorillas, another large herbivore, captive moose (*Alces alces*), maintained a stable intake of NPE and allowed protein intake to vary when they were restricted to a diet that did not allow them to reach their intake target [Felton et al., 2016]. Overall, these studies demonstrate that animals balance nutrient intake in general and employ rules of compromise when required. The consequences of these compromises are, however, not well understood, though it is probable that health problems ensue, especially when compromises occur over longer timeframes [Simpson & Raubenheimer, 2012]. If so, an animal must compromise to reduce the trade-offs between over-ingesting some important nutrients while under-ingesting others [Raubenheimer & Simpson, 1997]. Under-ingesting critical nutrients is hazardous to health, though deficits may be tolerated in the short term (e.g. during seasons of food scarcity; [Vogel et al., 2012]). Over-ingesting nutrients may also be costly, as they occupy limited gut capacity; evidence in non-primates suggests that compromise may have long-term health consequences [Simpson & Raubenheimer, 2012]. Animals may also incur costs from strategies that require ingestion of plant secondary metabolites (e.g. toxins), indigestible components (e.g. fiber or chitin), or that involve risky foraging behaviors (e.g. risk of predation). Not much is known about health problems in natural populations, however, though humans – who appear to strictly regulate protein intake – often consume excessive carbohydrates and fats, a strategy that may underlie the present obesity epidemic [Simpson & Raubenheimer, 2012].

Overall, an animal will demonstrate a *nutritional strategy*, a balanced intake with or without particular rules of compromise and prioritization of one or more nutrients, to approximate, as closely as possible, its intake target. The animal will also demonstrate a *feeding strategy*, which refers to the feeding behavior and specific food items consumed, to reach a particular intake target. Nutrient intake targets, though, are not fixed and actually move on a trajectory over time and on different scales [Raubenheimer & Simpson, 1997].

Animals regulate nutrient intake to reach those moving targets using two mechanisms: sensory cues and modulatory feedbacks [Raubenheimer & Simpson, 1997]. Sensory cues allow the animal to assess a food's nutrient composition while modulatory nutrient feedbacks use physiological feedbacks of a recent meal to prompt an animal to seek a lacking nutrient or halt consumption once the target has been reached. The target can change with physiological time, as immediate expenditures and gains (i.e. exercise or eating food) will determine nutrient needs in the near future. Targets will also change over developmental time, as an animal's nutrient needs change in response to growth, reproductive effort, maintenance, and senescence. For example, data from Friggens et al. [1993] on lactating rats indicate that the female rats consume more food to maintain body protein content, but at the expense of body lipids. Maternal rat nutrient intake also represents a rule of best compromise where protein and energy intake are balanced as nutritional needs increase [Raubenheimer & Simpson, 1997]. Linked to the fact that an intake target changes over time, the *quality* of a food will also change; that is, its value to the consumer depends on the intake target, which reflects the consumer's changing nutritional status and needs). Finally, targets will change on an evolutionary time scale as natural selection shifts targets to take advantage of different food resources and evolved life history strategies. The GF allows an examination of how animals link feeding strategies to nutritional strategies. It may be

particularly helpful in studies of dietary generalists, whose flexible feeding behavior might obscure a consistent underlying nutritional pattern.

Laboratory and field studies using the GF indicate that generalists, despite wide and varying diets, balance and optimize nutrient intake when possible [Raubenheimer & Simpson, 1997; Simpson & Raubenheimer, 1997; Rothman et al., 2011; Johnson et al., 2013; Erlenbach et al., 2014]. For example, locusts made dietary choices that kept salt and protein+carbohydrates in a constant proportion. Generalists should also tolerate more variation around an intake target, as they are presumably better equipped to handle excess nutrients in imbalanced foods. For example, generalist desert locusts tolerate more deviation from their target than a specialist counterpart [Raubenheimer & Simpson, 1997]. Grizzly bear populations (*Ursus arctos*) in Alberta, Canada persist (though at lower densities than elsewhere), despite being unable to approximate their nutrient intake target during some seasons because of unbalanced nutrient compositions in available foods [Coogan et al., 2014]. A comparison of 28 wild boar (*Sus scrofa*) populations showed dietary intakes that varied widely in all three macronutrients (fat, protein and carbohydrate), particularly the percentage of energy sourced from protein [Senior et al., 2016]. It may be that generalists can substitute energy sources. For example, captive brown bears (*Ursus arctos*) selected diets that interchangeably used fats and carbohydrates to balance a steady protein intake content that maximized mass gain per unit of energy intake [Erlenbach et al., 2014]. Also, there may be fitness consequences to being a generalist. Simpson et al. [Senior et al., 2015] used a meta-analysis to examine how a mixed versus single-food diet affected the between-individual variance in fitness parameters. As the number of foods in the diets increases, the mean fitness of the consumers increases and the variance of those fitness measures between individuals decreases (though see Lefcheck et al. [2013], whose study found mixed results). In

other words, consuming a wider breadth of foods likely allowed individuals to more closely reach their individual-specific optimal nutrient intake target, thus reducing variation observed in mean fitness.

In summary, natural selection works on the level of nutrients, so analyzing patterns of food intake and their relationship to food availability should include examination of the nutrient level [Raubenheimer et al., 2009]. The geometric framework is nutritionally explicit (i.e. able to discriminate among nutritional constituents and their importance) and highly flexible, allowing for multiple parameters to be tested simultaneously and over varying scales of time and space [Raubenheimer et al., 2009]. It is also organismally explicit, allowing researchers to explore the link between an animal and its environment. This method can reveal which nutritional requirements are guiding the behavior of the animal in a given environment [Raubenheimer et al., 2009]. Nutritional ecology provides a powerful, informative framework for studying foraging behavior and can be used to quantify the relationship between an animal and its foraging landscape.

CHAPTER 2. CHARACTERIZING THE NUTRITIONAL ECOLOGY OF ADULT FEMALE BLUE MONKEYS IN KAKAMEGA FOREST, KENYA

INTRODUCTION

Diet is fundamental to any animal's biology, and is related to its foraging behavior; indeed, the search for food can occupy a large part of an animal's active period and determine where it goes. Early characterizations of primate diets focused on the foods included, either the main constituent or the overall breadth of the diet, and researchers categorized animals accordingly (e.g. frugivorous vs. folivorous, generalist vs. specialist). More recent studies have focused on nutritional intake, thus characterizing dietary variation in new ways [Raubenheimer, et al., 2014; Simpson & Raubenheimer, 1995, 2012]. Food items (species specific plant parts, fungi, or animal prey) are packages of nutrients with various compositions. By studying dietary variation at the level of both food items and nutrient intake, researchers can link patterns of food availability in the environment to patterns of food item consumption to patterns in nutrient intake. For example, Rothman et al. [2007] demonstrated that two populations of gorillas (*Gorilla beringei*) living in environments with different food characteristics consumed different items, yet showed little variation in nutrient intake. Felton et al. [2008, 2009c] found that spider monkey (*Ateles chamek*) diets varied across months in energetic value, even though fruit was consistently a main component. As these examples illustrate, variation in diet composition in terms of food items may not reflect variation in terms of nutrients, and vice versa.

While researchers have long studied how seasonal food availability in the environment relates to diet selection and thus to variation in food item types, more recent studies aim to explore these patterns at the nutrition level as well. For example, seasonal changes in diet means

nutritional variation in some primates: gorillas (*Gorilla beringei*) varied protein intake between leaf-dominated versus fruit-dominated seasonal diets [Rothman et al., 2011], black howler monkeys (*Alouatta pigra*) seasonally interchanged lipids and non-structural carbohydrates (TNC, or sugars) as an energy source [Righini et al., 2017], while sifakas (*Propithecus verreauxi*) consumed more TNC, structural carbohydrates (NDF), fat and overall energy during the late wet season compared to the early wet and dry seasons [Koch et al., 2017], and aye-ayes (*Daubentonia madagascariensis*) consumed less overall energy, and smaller percentages of available protein and crude fat, but a higher percentage of NDF during the cold wet season compared to hot (dry and wet) seasons [Sterling et al., 1994].

While some nutritional variation relates to seasonal changes in available food, age-sex class may be another source of variation among individuals. For example, per unit of metabolic body mass, juvenile and adult female gorillas consumed more food and protein than did adult male silverbacks, with differences attributable to growth and reproductive needs respectively [Rothman et al., 2008]. In orangutans (*Pongo pygmaeus wurmbii*), flanged adult males had the lowest macronutrient and energy intake (per unit body mass) compared to all other age-sex classes, while immatures had the highest. On an absolute basis, though, there were no differences in macronutrient and energy intake, except for protein intake, which was significantly higher for unflanged males than for adult females and immature males [Vogel et al., 2017].

Not all variation in the diet translates into variation in nutritional intake. For example, humans have the most variable diets of all primates, and yet nutrient intakes vary little in protein content [Simpson & Raubenheimer, 2012]. Similarly, Peruvian spider monkeys (*Ateles chamek*) consumed a diverse array of fruits but their daily diets contained similar amounts of protein [Felton et al., 2008, 2009]. It is possible that flexibility in diet at one level, especially in terms of

food choice, actually serves to reach a common goal, with little variation, at another level, namely nutritional intake.

As dietary variation can differ on multiple levels, researchers can now move beyond the traditional categories of generalist vs. specialist. Indeed, Machovsky et al. [2016] suggested a new way to describe diet using a *multidimensional nutritional niche*. Using nutritional geometry, a researcher can classify an organism across multiple, non-exclusive levels (Figure 2.1). One level is food composition. If an animal consumes a diet composed of food items spanning a wide range of nutritional composition, then the animal may be considered a food composition generalist, since it subsists on a nutritionally diverse menu. This classification may be analogous to what is normally considered an omnivore's diet. The next level is the nutritional intake composition. If an animal consumes a diet that varies little in nutritional composition, then that animal can be considered a nutrition specialist. Considering multiple levels together allows one to describe an animal's multidimensional nutritional niche, providing a more nuanced view of dietary variation, how it relates to food resources and nutritional flexibility of an organism.

Feeding choices not only influence variation in diet and nutrient intake, but also other aspects of a primate's behavior, especially movement patterns [Chapman, 1988; Clutton-Brock, 1977; Doran, 1997; Isbell, 1991; Symington, 1990; Vedder, 1984]. Specifically, variation in daily path length (a proxy for energetic output) may reflect the consumption of fruit. For example, 3 of 4 groups of diademed sifakas (*Propithecus diadema*) increased daily path length (DPL) with an increase in fruit+seed consumption [Irwin, 2008]. Black crested gibbons (*Nomascus concolor jingdongensis*) traveled farther when they spent more time feeding on fruit [Fan & Jiang, 2008]. Similarly, black and gold howler monkeys (*Alouatta caraya*), increased DPL when fruit was highly available and they consumed more fruit and decreased DPL when

they ate more young and mature leaves [Raño et al., 2016]. Since many habitats in which primates occur experience seasonal fluctuations in fruit and other food types such as young leaves, food availability might also relate to DPL as animals adjust their travel to access seasonal food resources. Besides temporal food availability, spatial distribution of food should be linked to movement patterns in group-living primates, with further complexity added by group size [Chapman & Valenta, 2015; Clutton-Brock, 1977; Janson & Goldsmith, 1995]. All else equal, larger groups are expected to travel longer, faster, or use larger areas than smaller groups in their effort to meet their group collective nutrient needs [Snaith & Chapman, 2007] and this should be especially true for frugivores, whose food sources are often patchily distributed [Clutton-Brock, 1977; van Schaik & Janson, 1988; Wrangham et al., 1993; Chapman et al., 1995; Janson & Goldsmith, 1995]. Some primate populations show evidence of a positive relationship between group size and DPL (chacma baboons (*Papio ursinus*, [Hoffman & O'Riain, 2012]), Sulawesi black crested macaques (*Macaca nigra*, [O'Brien & Kinnaird, 1997]), mantled howler monkeys (*Alouatta palliate mexicana*, [Aguilar-Melo et al., 2013]), though other populations do not (nonlinear relationship in Colombian wooly monkeys (*Lagothrix lagothricha*, [Stevenson & Castellanos, 2001]) and no relationship in Tonkean macaques (*Macaca tonkeana*, [Riley, 2008])).

In this study, I aimed to evaluate dietary choices and their effect on nutritional intake and daily path length in the blue monkey (*Cercopithecus mitis*). Though often categorized as frugivorous, based on the main constituent of their diet [Lawes et al., 2013], blue monkeys have relatively capacious hindguts and slow retention times that allow them to ferment and digest substantial amounts of folivorous material as well [Blaine & Lambert, 2012; Bruorton et al., 1991; Bruorton & Perrin, 1991; Lambert, 2002, 2015]. Perhaps better characterized as

omnivorous, they are generalist feeders that consume many types of food items (fruits, flowers, young leaves, animal matter, fungi, bark, stems, mature leaves and exudate [Lawes et al., 2013]) from a wide variety of plant species (e.g. with values up to 104 species in a given population; [Coleman & Hill, 2014a; Cords, 1987; Lambert, 1998]). The proportion of particular foods in the diet (based on time, fecal analysis and stomach content analysis) can vary widely among populations and across time (fruit (28-91%), leaves (2-52%), flowers (0-14%), animal matter (0-38%; [Coleman & Hill, 2014a]). While it is clear that blue monkey diets are highly variable in terms of food item type, it is not known whether those diets are also variable in terms of nutrition.

To investigate this question, I examined variation in the diets of adult female blue monkeys with three goals. First, I characterized their diet in terms of composition, identifying important foods (those contributing ≥1% of caloric intake over the study period and foods that collectively dominate the diet), and how consumption of specific items related to their availability (combination of vegetation surveys and plant phenology). I predicted that abundant plant species with edible fruits or young leaves would constitute the most important foods. I also expected that the diet would change in response to fluctuations in food availability, specifically that fruit in the diet, as the main constituent, would be positively related to its availability, and that young leaves, as the second most important constituent, would be negatively related to fruit availability and positively related to young leaf availability. Second, I evaluated the diet in terms of the multidimensional nutritional niche, specifically the degree of variation in nutritional intake relative to food intake, and how these monkeys fit in the nutritional intake generalist-specialist spectrum. Third, I examined one consequence of variation in diet, namely its effect on daily path length (DPL). I predicted that DPL would reflect the amount of fruit, the main constituent, in the

diet, as well as other factors, such as food availability, caloric intake and group size. A previous study found that groups' travel distances (measured by hourly "center of mass") were negatively related to group size and the relationship was not because of differences in habitat quality [Cords, 2012] . Additionally, when DPL was analyzed using individuals' movements, females in smaller groups traveled farther than larger groups in the morning and afternoon (no difference in midday), attributable to smaller groups travelling farther to reach specific food resources on the edges of their home ranges [Cords, 2012]. I expected to confirm these patterns and predicted DPL would be longer for smaller groups. Finally, I compared the dietary variation I documented to previous reports from the same study population and other populations of blue monkeys.

METHODS

Study site: The study site was a ca. 2 km^2 area of the Kakamega Forest, western Kenya, located near the Kakamega Forest Station (0^o 19' N, 34^o 52' E), a site of long-term study of the species [Cords, 2012]. The Kakamega Forest is a ca. 238 km^2 patch of semi-deciduous rainforest (1650 m elevation) that was once part of more continuous Guineo-Congolian rainforest that spanned sub-Saharan Africa [Kokwaro, 1988]. During the study period (January-September 2015), rainfall averaged 222 mm per month with fluctuations generally matching longterm norms (Figure 2.2). As a result of human interference that preceded the colonial era and continued through both a 1930's gold rush and logging concessions in 1930-40s, the forest is a mosaic of various habitat types on a small scale [Mitchell & Schaab, 2008; Mitchell, 2004; Mitchell et al., 2009]. Fischer et al. [2010], in the most comprehensive inventory, reported 986 species of vascular plants, including six species endemic to Kakamega Forest.

Previous research by the BIOTA East Africa project classified the forest into plant communities that represented different successional stages, mostly determined by past anthropogenic disturbances and soil microclimate [Lung & Schaab, 2006; Mitchell & Schaab, 2008; Mitchell, 2004; Mitchell et al., 2009]. The southern part of the forest, where this project took place, comprised old secondary forest with important trees such as *Prunus africana* and *Antiaris toxicaria*, as well as plantation forests dominated to various degrees by *Maesopsis eminii*, *Bischofia javanica*, *Eucalyptus saligna*, *Pinus patula*, *Cupressus lusitanica* and *Psidium guajava*.

For the purposes of this study, I simplified BIOTA's classification and identified three habitat types that generally had discrete borders and reflected the local history of human intervention [Mitchell, 2004; Mitchell et al., 2009]. Differences were obvious on the ground according to the structure of the vegetation and/or the presence of particular edge-specialist trees (such as *Harungana madagascariensis* and *Solanum mauritianum* on the edge of the near-natural forest*)*. *Near-natural forest* comprised mainly mature secondary growth of native trees, although a few non-native species such as *Bischofia javanica* grew intermittently, especially along trails, as a result of experimental plantings by the colonial forest department. The 7.87 ha *village forest* was located in the center of the study site and included scattered Kenya Forest Service buildings and roads and a 1.58 ha tree nursery (Figure 4.1, [Chap 4]). While land cover included grass and heterogeneous tree cover that was sparse compared to the adjacent near-natural forest, the trees were dense enough that monkeys could travel through the village via arboreal pathways, and large enough to allow animals to congregate for social activity like grooming. *Farm/plantation forest* occurred mainly in the southern part of the study site, though a small (1.14 ha) patch occurred close to the village forest (Figure 4.1, [Chap 4]). Farm/plantation forest was mainly

monocultures of exotic species (*Bischofia javanica, Grevillea robusta)* and abandoned farmland overgrown by guavas (*Psidium guajava)* with large, dispersed *Eucalyptus saligna.*

Subjects: The study population of blue monkeys had been under study since 1979, with the number of individuals monitored at one time growing over the years as groups slowly grew and fissioned [Cords, 2012]. Group density stayed relatively constant, as study groups expanded the area that they used [Cords, 2012, unpublished]. Population density also remained relatively stable (1979-1981 estimate: 198 ind/km^2, 1994-1998 estimate: 220 ind/km^2; 2006-2010 estimate: 192 ind/km^2 [Fashing et al., 2012; Fashing & Cords, 2000]). The growth of the study groups suggests that monkeys had access to adequate food and nutrition over the long term to maintain body condition, as well as reproduce (births occur seasonally, every 2-3 years per individual; [Cords & Chowdhury, 2010]).

Subjects were 24 adult (parous) females, 8 from each of three study groups, aged 6.9-25.0 years (mean 13.8 ± SD 4.5 years), of differing ranks and reproductive states. The groups' home ranges varied in size (23.9 ha GN, 41.8 ha GSC, 52.3 ha TWS, Table 3.1, [Chap 3]) and habitat composition (e.g., near-natural forest accounted for 56-92% of each home range, Figure 4.1, [Chap 4]).

Data collection

Field assistants: Field assistants trained in behavioral observation for 3 months prior to the study period. Experienced field assistants from Cords' longterm field project, with many years of fieldwork experience, trained the study assistants almost daily in monkey and plant identification. I taught assistants to collect behavioral data, as well as food and fecal samples. The team was quizzed weekly to assess training progress. I determined that training was

complete when all assistants correctly identified (>95%) monkeys and plants and correctly coded behavior data in a day-long field test.

Behavioral observations: A team of observers conducted all-day focal follows [Altmann, 1974] on each subject approximately twice a month for 9 months, spacing repeated samples of each individual at >1 week intervals (mean 15.4 ± SD 5.9 days, N=347 intervals). All-day focal follows are recommended for studies of nutritional ecology because they allow the most accurate record of daily diet [Felton et al., 2009; Rothman et al., 2012; Rothman et al., 2013]. The team started looking for monkey groups at 6:30 AM and generally concluded the day's observations at 18:30, though exact timing depended on weather and lighting conditions, which could significantly obstruct visibility during the rainy season. During follows, subjects occasionally went out of sight, but average "in-sight" time was 9.1 ± SD 0.2 hr and out of sight averaged 0.7 ± 0.2 hr (not including time in the morning searching for group and focal subject, Table 2.2).

Using tablets running Microsoft Office 365's Excel application, team members recorded the start and end of each focal animal's feeding bouts with a time stamp, as well as the species and part of all plant food items and morphotype of insects. Feeding bouts started when food first touched a subject's mouth and continued as long as she was taking bites and/or chewing. Team members did not stop bouts if she continued to hold the food between these acts of ingestion (there were often brief pauses of a few seconds); however, if a female paused for vigilance or other alarm responses, team members stopped the bout. Observers noted how individuals processed food (e.g. spit seeds or peeled stems before consumption) and quantities eaten using standard units that were easy to differentiate (e.g. one *Psidium guajava* fruit, one *Mimulopsis solmsii* leaf, a 1-inch section of *Bischofia javanica* stem [Rothman et al., 2012, 2013]). With a continually updated list of blue monkey plant foods, observers were able to identify most plants

in the field; when they were unable to identify a plant, they obtained a sample and consulted local forest guides for identification (this happened rarely).

Movement: To track each subject's movement throughout the day, observers recorded GPS coordinates (Garmin GPSMAP® 60 CSx, with an error of ±5 m or less) at 30 min intervals, on the hour and half hour, standing 0-3 m from the subject's position on the ground (or using an imaginary plumb line from her position in the tree to the ground). If a subject was out of sight in a known location (e.g. hidden in vines), we still took the GPS point. Observers missed some scheduled GPS records when the focal subject's exact location was unknown (i.e. at top of large tree) or when she was lost from view entirely. In addition to the GPS records of the focal animal, observers also recorded GPS locations of the group, once in the morning and once in the evening. In the morning, when observers first found a group by identifying an adult female, observers recorded that female's location as an approximation of the group's location. In the evening, just before leaving the group, observers recorded the location of the focal animal, or if the focal animal was lost, the location of any adult female belonging to the group, again as an approximation of the group's location.

Monkey food collection: I collected samples of plant foods by hand-picking, pole sawing or knocking from trees. Whenever possible, I collected samples from the very same plants that monkeys used for feeding. To identify insect morphotypes, I used direct observation and secondary cues (e.g., stereotypic behavior like rolling hairy caterpillars on branches or unrolling dead leaves to access pupae inside). I collected insect samples from vegetation, and euthanized them via decapitation or ethanol exposure [Ozanne & Bell, 2003]. Insect collection was opportunistic, as feeding on insects was quick and precluded collection. Social insects (like ants) could sometimes be collected at the time of feeding observation.

I dried plant and insect samples in a solar-powered dehydrator (custom designed by Bruce Cameron, Nango Solar Limited, Kisumu, Kenya with a fan at the bottom of the unit and air vents). Sample drying occurred primarily during the day, and sometimes throughout the night when the battery was sufficiently charged. The dehydrator was set to a constant temperature of 55 °C [Rothman et al., 2012]. Samples typically dried over the course of a few days (range: 1 day to 1 week). I shielded samples from sun exposure and discarded any samples that were moldy after the drying process (this happened rarely). During the dry season (January-early March), I dried some mature leaf samples in a warm, dark shed that blocked all sunlight [Rothman et al., 2012]. Dried plant samples were either milled (required for export permit) by hand at the research site, or for tougher materials, at the Kenya Agricultural & Livestock Research Organization, 16 km away in Kakamega town, using a 1-mm sieve [Rothman et al., 2012].

Fecal sample collection: I collected a fecal sample (approximately 5-10 ml, from the ground or off vegetation) from a given female one day after each focal follow using sterile Corning 15 ml plastic tubes. I poured ethanol into the tube to cover the sample and allowed the sample to sterilize for a minimum of three days, after which I poured off the ethanol [Rothman et al., 2012]. Fecal samples were dried in the tube at the Kenya Agricultural & Livestock Research Organization, as this facility had a grid-powered oven that could dry the ethanol-soaked fecal samples day and night at a constant 55 ° C.

I sealed the dried samples in the tube with Parafilm for future analysis to assess baseline digestibility of fiber (see *Nutritional analyses* below). If it was not possible to obtain a sample from the previous day's focal subject, I tried to collect a sample from another adult female in the same group, which allowed me to assess a mean value for fiber fermentation.

Unit weights: I organized food collections by species-specific food parts collected on a particular day. For each species- and part-specific collection, I tried to record the weights of 50 units of each food item (before drying) within 24 h (and usually within 6-12 h) of collection in the field. Before weighing, I processed the food items in a way that matched what I observed the monkeys doing (e.g. peeling the stem or selecting only inner seeds). I weighed units by the same observably consistent amount recorded during focal follows. When a collection yielded less than 50 units, I weighed as many as possible. When a collection yielded more than 50 units, I randomly chose 50 units for weighing. I recorded weights using a portable electric scale (American Weigh, model Ac-100, accuracy guaranteed to 0.01 g). If a food unit was too small to be weighed individually (e.g. ants), I weighed batches of 2-10. I periodically confirmed the accuracy of the scale with an object of known weight.

I did not record unit weights for a collection event if 50 unit weights had been recorded for the same species-specific food item within the past month [Rothman et al., 2012]. For each collection comprising 50 units, I calculated a mean unit weight. For collection events comprising less than 50 unit weights, I binned consecutive collection events until they contained 50 unit weights, and then calculated the mean [Rothman et al., 2012].

Vegetation surveys: I measured vegetation cover using a random transect method [Ganzhorn et al., 2011; Marshall & Wich, 2013]. I combined data from transects measured in 2014, as part of the longterm dataset collected by Cords and her team, with new transects measured as part of my study. All transects measured 100x10m^2 [Ganzhorn et al., 2011] in the groups' home ranges. My team measured all trees and herbaceous plants with DBH (diameter at breast height) ≥ 5 cm in the transects that were established during my study. The 2014 transects included only trees with DBH≥10 cm, so my team relocated those transects and measured small

trees and herbaceous plants with DBH ≥5 and <10 cm, which was important for assessing the availability of foods from herbaceous plants. The number of transects ensured that (i) each group's range contained transects that represented habitat types in proportion to their abundance in the range, and (ii) there were at least 5-10 transects per habitat type [Ganzhorn et al., 2011] and their combined area accounted for ≥3-7% of the home range, commonly used coverages [Chapman, 1990; Chapman et al., 1994; Estrada & Coates-Estrada, 1984; Foerster et al., 2012; Harrison, 1983; Loiselle & Blake, 1990; Raemaekers, 1980; Whitten, 1982]. Overall, there were 36 near-natural forest transects and 10 farm/plantation forest transects. For the village forest habitat, where tree coverage was heterogeneous (plants either clumped or planted in rows along roads), random transects did not appear to assess basal area of plants very accurately. Therefore I measured all trees and herbaceous plants with DBH≥5 cm in the village area used by the study groups (TWS, GN, 6.6 ha) and scaled the values to make them comparable to transect data on a per hectare basis.

Plant phenology monitoring: Two assistants alternated phenology scoring at 2 week intervals. They scored the availability of fruit and young leaves for 10 stems (typically) of each of 33 main food plant species (those constituting >0.5% of feeding time in ≥3 of 23 group-years (2007-2011) in which adult female feeding behavior was documented by focal animal samples, as well as some unique trees that were heavily used (Cords, unpub.)). One species, an exotic oil palm (*Elaeis* sp.), existed only as a single tree in the village, so I was limited to one bi-weekly score for this species. For each plant part, the assistant assessed the phenophase using a semi-quantitative (0-4) scale (0=none, 1=1-25% of maximum capacity, 2=26-50%, 3=51-75%, 4=76-100%). The assistant also assessed the proportion of fruit that was ripe (0% ripe, 25%, 50%,

100%). I then multiplied fruit capacity score by proportion ripe to assess ripe fruit availability (e.g. 50 % fruit capacity x 25 % ripe=13 % ripe fruit availability).

Food availability index: I then calculated a plant-part specific food availability index (FAI) for every bi-weekly phenology scoring and for each group [Chap 2]. For each FAI score, I averaged the basal area (BA) of each tree species from vegetation surveys in a particular habitat type, then multiplied this measure by the mean phenology score of that species, and added these products together across all phenology species. I computed composite scores for each group by weighting the habitat-specific phenology indices according to their representation in the group's home range.

Wet chemistry analyses: I conducted lab work in the Rothman Nutrition Lab, Hunter College, City University of New York. I measured the percentage composition (per gram dry mass) of the following nutritional parameters in monkey foods: structural carbohydrates (cellulose, hemi- cellulose, lignin, measured via neutral and acid detergent fiber (NDF and ADF) and acid detergent lignin analyses (ADL)), available protein (hereafter referred to as protein, subtracting acid detergent insoluble protein from crude protein amount from combustion), ash (i.e. minerals, measured through combustion and correcting for fiber bound ash) and crude lipid (via ether extraction; [AOAC, 1990; Conklin-Brittain et al., 2006; Licitra et al., 1996; National Research Council, 2003; Palmquist & Jenkins, 2003; Rothman et al., 2008; Rothman et al., 2012, 2013]). I computed percentage of total non-structural carbohydrates (TNC, i.e. sugars) by subtracting from one the sum of NDF (i.e. structural carbohydrate estimate), protein, lipid and ash ([Rothman et al., 2012], Appendix I).

An animal's gut physiology determines its ability to digest fiber via microbial fermentation. Captive blue monkey females had a mean gut retention time of plastic markers of

20.6 hr ±12.8 SD hours [Lambert, 2002], so I related an observed daily diet to the fecal sample collected the following day. To determine energetic gain from fiber, I compared the lignin content in the daily diet to the corresponding fecal sample to calculate the fraction of the ingested fiber that was fermented and subsequently digested [Fahey & Jung, 1983; Rothman et al., 2012; Van Soest, 1994].

I calculated fiber digestibility coefficients as follows [Conklin-Brittain et al., 2006; Rothman et al., 2008]:

For fiber fermentation on a dry matter basis (NDF_{DM}):

NDF digestibility $_{DM} = 100 - [\frac{100 * proportion\ of\ ADL\ in\ diet}{proportion\ of\ ADL\ in\ feces} * \frac{proportion\ of\ NDF\ in\ feces}{proportion\ of\ NDF\ in\ diet}]$

where ADL=acid detergent lignin analysis

NDF=neutral detergent fiber analysis

DM=dry matter basis

Near Infrared Reflectance Spectroscopy (NIRS) analysis: In addition to wet chemistry, I used NIRS to analyze plant food nutritional composition [Rothman et al., 2012]. A sample irradiated with near-infrared light reflects a unique vibrational energy spectrum (within the 800-2500 nm range) based on chemical bonds. In particular, O-H, N-H, C-H and S-H bonds produce strong NIRS signals in spectra. These spectra are then matched and calibrated against reference values determined via traditional wet chemistry analysis. Calibrated spectra are grouped according to plant parts to create predictive equations, which allow estimation of the nutritional values for samples of the same plant part. This technique had been shown to measure accurately

the nutritional content of primate diets [Rothman et al., 2009, 2012], and greatly reduces both time and cost of analysis.

Additional nutritional values: Blue monkeys consumed eight human foods: chicken egg, maize, *ugali* (cooked maize flour), cabbage, watermelon, sweet potato, orange and sugarcane. I analyzed maize and *ugali* samples in the lab (Appendix I), and for the other six foods, used nutritional parameters from the USDA (https://ndb.nal.usda.gov/ndb/). Nutritional values of insect samples were determined using wet chemistry lab techniques by P. Wakaba at the Kenya Agricultural & Livestock Research Organization, Muguga campus. I was not able to collect some food items (together representing 2.4% of total observed feeding time; Appendix II). For the nutritional value of these food items, I used the means of part-specific values, as determined by my laboratory analyses.

Daily nutrient intakes: I calculated daily nutritional intake (in grams) per focal follow by multiplying the observed quantity of food consumed (number of units x unit weight) by the food's nutritional value (percentage composition of a given macronutrient, e.g. % protein per unit weight), then summing these values across all foods consumed. I reported the following measures (in g, dry matter basis): TNC, lipid, protein, NDF, ADF, ADL, ash and total food (sum of TNC, lipid, protein, NDF and ash). I then converted macronutrient intakes (in grams) to energetic values (kcal) using the following conversions: 4 kcal/g for non-structural carbohydrate, 4 kcal/gram for protein, 9 kcal/g for lipid and 3 kcal/g for fiber [Conklin-Brittain et al., 2006]. The caloric value of fiber was adjusted by multiplication with a fiber digestibility coefficient specific to each group (GN group: 0.37, N=72; TWS group: 0.39, N=66; GSC group: 0.22, N=67; see Wet Chemistry analyses above [Conklin-Brittain et al., 2006]). I reported the

following measures (in kcal): TNC, lipid, protein, NDF and total energy (sum of TNC, lipid, protein and NDF).

Data analysis

I used R, version 3.3.2 [R Core Team, 2016] for statistical and some graphical analyses, specifically the R packages MASS [Venables & Ripley, 2002], lme4 [Bates et al., 2015], lmerTest [Kuznetsov et al., 2016], ggplot2 [Wickham, 2009] and piecewiseSEM [Lefcheck, 2016]. I validated all models by checking the residual distribution, plotting residuals against predictors and plotting a Q-Q plot [Ieno & Zuur, 2015; Zuur et al., 2009]. For any model with multiple predictors, I verified that they were not collinear by examining Pearson correlation coefficients using a cut-off of 0.8 [Ieno & Zuur, 2015; Zuur et al., 2009].

Relationship between diet and food availability: The two main constituents of the blue monkey diet are fruit and young leaves [Lawes et al., 2013]. To explore how fruit in the daily diet related to fruit availability, I was interested in two measures: percentage of fruit in the diet (based on kcal), which indicated the degree to which subjects focused their diets on fruit, and absolute fruit intake (kcal), which indicated direct relationship between fruit intake and fruit availability. I ran two linear mixed models with restricted maximum likelihood (REML; [Bates et al., 2015; Kuznetsov et al., 2016]), with a Gaussian distribution [Zuur et al., 2009]. I transformed the absolute amount of fruit in diet using its square root, which normalized the distribution [Ieno & Zuur, 2015; Zuur et al., 2009]. The fixed effect was the FAI of fruit (divided by 1000). I included Subject ID nested in Group as random effects (N=371 female-days). I tested the significance of the fixed effect by comparing the model to a null model with only random effects, using a likelihood ratio test with maximum likelihood (LRT). All LRTs mentioned henceforth also used maximum likelihood. Both models had N=371 female-days.

To explore the determinants of young leaves in the daily diet, I carried out a similar analysis but included both FAI of fruit (divided by 1000) as well as FAI of young leaves (divided by 1000) as fixed effects. Including both FAI measures allowed me to examine whether young leaf consumption was supplementation to low fruit availability or a response to young leaf availability. I transformed the dependent variable using the square root (kcal of young leaves in daily diet) to normalize the distribution (N=371 female-days; [Ieno & Zuur, 2015; Zuur et al., 2009]). I compared the full model to the null model with only random effects using a LRT and I reported the full model summary since it reflected both predictors of interest and their significance [Forstmeier & Schielzeth, 2011]. I did not examine the percentage of young leaves in the diet because it was highly correlated with percentage of fruit in the diet.

In addition to examining whether fruit (or young leaves), as a category, was related to its overall availability, I also examined how consumption of species-specific fruit (or leaves) were related to overall fruit (or young leaf) availability. I calculated bi-weekly selection ratios that represented the proportion of a species-specific item in a day's diet (by kcal) divided by the proportion of the total FAI represented by that item. I averaged selection ratios across the days in which a species-specific fruit or young leaf was recorded in the daily diet. Selection ratios were limited to the 33 species that were monitored for phenology, though not all were monitored for fruit or young leaves (e.g. *Cupressus lusitanica* was not scored for fruit and *Psidium guajava* was not scored for young leaves). Mean selection ratios above 1 indicated that the food item was selected (i.e. consumed disproportionately to its availability). Ratios of 1 indicated that the food was eaten in proportion to its availability.

Characterizing the multidimensional nutritional niche: The multidimensional nutritional niche, or the diet in general, can be visualized using Right-Angled Mixture Triangles (RMTs), a

common tool in nutritional geometry [Raubenheimer, 2011; Raubenheimer et al., 2015]. This geometric representation is a variation of a ternary plot (also called a de Finetti diagram or triangle plot). The advantage of a RMT plot is that it is right-angled and reading values of points is more intuitive than equilateral triangle plots. The RMT is based on a Cartesian plane, with the implicit third axis (*i*-axis) a series of negative-sloped isoclines from 0% to 100%. The axis values of a particular point on the plot must sum to a constant, K, usually 100%. Thus, it is easy for one to see the x and y values of a point and then deduce the implicit value of the third axis by K-x-y. For nutritional geometry, the RMT is particularly well suited because there are three macronutrients that contribute to energy intake: lipid, protein and carbohydrate. A nutritional space is defined by a set of points bounded by a minimum convex polygon. An organism can arrive at any nutritional intake within the nutritional space, defined by food items, by consuming a mixture of those food items.

To visualize the contrast of the diet in terms of food composition against the nutrient intake composition, I plotted both levels of compositions on RMTs. I first plotted all the food items consumed by blue monkeys and drew polygons to represent the diet of each group. I then plotted three points that represented the mean nutrient intake of the three study groups.

To better characterize the variation in the nutrition intake composition, I also created RMTs with mean nutrient intake composition of individuals. I connected with a polygon the individual means within a group to visualize the mean range of the nutrient intake by each group's females. To explore whether diet intake was a result of active regulation of nutrient intake (diet selection) or a result of passive consumption of available foods, I created an additional RMT that compared the average nutrient intake by females in a group with the intakes expected if females consumed diets based on the relative availability of food items

[Raubenheimer et al., 2015]. I calculated the expected diet using twice-monthly FAI data, weighting each species-specific food item by its FAI score, and then multiplied those scores with nutritional value data of foods items (e.g. an imaginary FAI score of 100 for a given fruit was treated like "grams" and multiplied by the percentage of NDF, TNC, protein and lipid for that fruit, then converted from grams to calories as described in the *Daily intake diet* section above). I then calculated an overall average intake for each group (N=16 per group).

In addition to the RMTs, I ran linear mixed models for nutrient intake. I created eleven models, one each for these response variables of daily intake: total energy (kcal), non-protein energy (kcal), lipid (kcal), protein (kcal), NDF (kcal), TNC (kcal), food (g, DM basis), NDF (g, DM basis), ADF (g, DM basis), ADL (g, DM basis) and ash (g, DM basis). NDF was tested using both the kcal value and the gram value since there were group-specific differences in fiber digestibility (i.e. there could be significant variation in caloric intake of NDF, but not dry weight intake, or vice versa). I used Group as a fixed effect and changed the baseline comparison group to assess all possible pairwise differences. I used Subject ID as a random effect to control for repeated measures.

Finally, to explore how seasonality of fruit might have driven variation in nutrient intake, I again used linear mixed models for nutrient intake. I created eleven models, one each for the same response variables listed in the previous paragraph. For the fixed effect, I used fruit availability (high vs. low), which was defined for each two week period according to whether the fruit FAI score fell above or below the mean value for the study site (Figure 2.3). I used Subject ID nested in Group as random effects. All models were based on N=371 female-days.

Predicting daily path length: I calculated daily path lengths by summing the distances between consecutive GPS points [Dutch, 2016; Karney, 2011]. If a GPS point was missing (e.g.

subject was lost), I interpolated by connecting the prior and subsequent points. If a subject was not found first thing in the morning, or lost before the end of the day, I also extended her daily path through extrapolation, connecting her first GPS location to where we first found the group in the morning, and/or her last GPS location to where the group was left at the end of the day (ca. 6:30 pm). DPL measurements were based on a mean of 11.0 ± 0.6 group observation hrs per day (range=8-12 hr, N=371).

Because the adjustments above were straight-line connections, sometimes spanning several hours, they would underestimate the actual lengths of curved paths. I investigated this potential bias in two ways. First, I found no significant relationship between DPL and number of GPS points in a day (a measure of time spent with a group; OLS regression, F-statistic (1, 369)=1.87, N=371, p-value=0.17). Nevertheless I included the number of GPS records (for a given day) as a control variable in the final model. Second, I compared measures of DPL as described above to a measure that did not involve interpolation or extrapolation. This measure was based on deviations from average patterns. Using data only when 2 consecutive GPS locations were separated by 30 min, I calculated the mean distance traveled for every 30-min period of the day across all subjects (e.g. mean distance traveled between 8-8:30 am). I then expressed a particular subject's deviation from the mean distance for every half hour block in which she was observed, and averaged these deviations across the blocks in which she was observed on a given day. A female with a positive score thus traveled more than average, whereas a negative score indicated less than average travel across the day. Daily deviation scores correlated significantly and positively with DPL (OLS regression, F-statistic (1, 369)=1734, N=371, adjusted R^2=0.82, p-value: < 2.2e-16). I therefore ultimately chose to use DPL as the

response variable in further analyses as it was more intuitive and would facilitate comparison with other studies.

To evaluate which factors predicted daily path length, I ran a linear mixed model with restricted maximum likelihood (REML; [Bates et al., 2015; Kuznetsov et al., 2016]), with a Gaussian distribution since response variables were normally distributed [Zuur et al., 2009]. The predictors of interest included daily group size (all adults and juveniles > 1 year old), centered FAI of young leaves, centered FAI of ripe fruit, percentage of fruit in the diet, and daily caloric intake (animals might move more when consuming more). Since FAI scores were group-specific, daily group size covaried with FAI. I centered the FAI scores on the group mean to remove the collinearity [Grace-Martin, 2015]. I included two control variables, namely monthly rainfall (heavy rains reduce movement) and number of GPS points (observation bias). Daily rainfall data came from Kenya Forest Service records of rainfall accumulating in a gauge between consecutive ~9 am readings. Daily caloric intake was calculated as described above (see *Daily diet intakes*). The number of GPS points accounted for time spent with the group and focal subject. Random effects included Subject ID nested within Group.

I fit the full model with all predictors and then compared the model to a null model (only random effects) using a LRT. Again, I reported the summary from the full model since it reflected all predictors of interest [Forstmeier & Schielzeth, 2011].

RESULTS

Vegetation composition in different habitat types: The near-natural forest and farm/plantation forest had similar mean BA (basal area) density of trees and shrubs (Table 2.1). In contrast, the vegetation in the village forest was relatively sparse.

The top five species (by mean BA) in farm/plantation forest dominated the species composition (88% of BA per ha). In contrast, the top five species were less dominant in the near-natural forest (51% of BA per ha) and in the village forest (50% of BA per ha). The near-natural forest had the highest species richness (82 species), followed by village forest (62 plant species) and farm/plantation (28 species). The top five species were different in each of the three habitat types, except for *Cupressus lusitanica* and *Bischofia javanica*, which were in the top five for both the village forest and farm/plantation forest.

Characterization of the diet on the food level: Of the mean 9.1 ± SD 0.2 hrs/day subjects were in sight during a focal follow (N=371 female-days, 15-16 per subject), females spent a mean 29.2% of time feeding (Table 2.2), with little variation across groups (TWS: 30.1%, GN: 29.6 %, GSC: 28.0%). Overall, subjects consumed 445 food items (435 species-specific plant parts, Appendix III, 9 insect morphotypes, and soil). Plant foods came from 128 plant species, not including human-derived food (e.g. watermelon, cabbage).

Overall, females spent most time feeding on fruit, followed by young leaves, mature leaves, flowers and flower buds (Figure 2.4). Each of these food item types (non-species-specific items) accounted for >5% of mean daily feeding time. Similarly, when I divided the females by group, fruit and then young leaves were the top two types, accounting for 71% (range=69%-74% per group) of feeding time (Appendix IV). However, females in different groups differed on their third type (GN: leaf bud, GSC: insects, TWS: flower and buds).

A similar pattern in diet composition emerged when I calculated the diet in terms of caloric value by food item type (Figure 2.4). As a population, females ate a diet with fruits as the main source of calories, followed by young leaves, then mature leaves, and finally exudate; each of these food types accounted for ≥5% of mean daily caloric intake. However, for females in

GSC group, the third most important source of calories was exudate and the fourth, mature leaves (Appendix IV). Also, for females in GN group and TWS group, the fourth most important source was leaf buds. Overall, when the diet was calculated by group, females had similar diets in terms of caloric contribution, with the most important food item type for all groups, fruit, contributing more than half the calories (51-60%, Appendix IV). All groups shared young leaves as the second most important food type. Together, fruit and young leaves contributed the majority of calories to the diet (76-78% per group).

While the most important (fruit, young leaf, and mature leaf) and some of the least important (human food, mushroom) ranked similarly regardless of whether I assessed diet composition by feeding time or caloric intake, some middle ranked food item types showed less consistency when assessed with alternative metrics. For example, exudate ranked fourth in terms of calories but eighth in terms of time, suggesting that it was an energetically dense food relative to feeding effort. Insects ranked tenth in calories but fifth in time, suggesting that females spent a disproportionate amount of time consuming them (~5%) relative to their caloric contribution to the total diet (<1%). Finally, flowers ranked fourth in time but sixth in calories.

Important food items: I defined important food items as those that contributed ≥1% of total calories consumed by females in a particular group over the study period (Figure 2.5). Though caloric value and nutritional composition varied among important food items, together they represented similar percentages of calories consumed by females in each group (GN 72%, TWS 73%, GSC 74%). However, the number of important food items varied among groups, and was especially low for GSC (GSC 12, GN 20, TWS 21). Many food items were important to multiple groups (Figure 2.6). TWS and GN shared the most items (9), while TWS and GN shared only three. GN and GSC shared four food items that were also important to TWS (i.e.

there were no uniquely shared foods between GN and GSC). Generally, species-specific fruits were the most important foods for each group: fruits accounted for 82% of the important foods for GN, 81% for GSC, and 78% for TWS. Particular leaves (young and mature) were the second most important type of food in two of the groups, accounting for 14% of GN's important foods and 16% of TWS's important foods. Gum accounted for 8% of GSC's important foods.

Relationship between food availability and food composition of diet: Percentage of fruit was positively and significantly related to its availability in the environment (Table 2.3, Figure 2.7a). A model with FAI of fruit as a predictor was significantly different than one with only random effects (LRT: X^2(df=1)=39.51, p=3.27e-10). Also, the square root of the amount of the fruit in the daily diet (kcal) was positively and significantly related to its availability in the environment (Table 2.3, Figure 2.7b). A model with FAI of fruit as a predictor was significantly different than one with only random effects (LRT: X^2(df=1)=18.45, p=1.75e-05). The square root of the amount of young leaves in the diet (kcal) was significantly and negatively related to both young leaf availability and fruit availability. A model with both predictors was significantly different from a null model (LRT: X^2(df=2)=32.48, p=8.84e-08; Table 2.3, Figure 7 c,d).

Selection ratios for species-specific fruit and young leaves: Of the 32 species of plant monitored for fruit phenology, 56% were positively selected (i.e. mean selection ratio >1) and 16% were not selected (i.e. mean selection ratio <1; Table 2.4). Subjects did not eat 19% of fruit species during the study period. Two species of fruit (*Polyscias fulva* and *Trilepisium madagascariensis*) were eaten, but were recorded as not available in the environment, and therefore it was impossible to calculate a selection ratio. Of the 26 species of plants monitored for young leaf phenology, 58% had mean selection ratio greater than 1 and 31% had mean

selection ratios less than 1. Subjects did not eat the young leaves of two species, *Cordia africana* and *Croton sylvaticus*, during the study period.

Characterization of the diet on the nutrient level: Females consumed a grand mean of 228 g (dry weight) of food per day, of which 41% was NDF, 30% TNC, 15% protein, 7% lipid, and 7% ash (Table 2.5). Expressed in terms of energy, the daily diet comprised 643.6 kcal, of which 42% was TNC, 23% lipid, 21% protein, and 14% NDF (grand means; Table 2.5).

Females in the three groups did not differ in terms of energy intake (Table 2.6, Figure 2.8). They also did not differ in NPE, protein and ash intake. However, females in different groups consumed significantly different caloric amounts of lipids, NDF, and TNC and different (dry) weights of NDF, ADF, ADL and total food (Table 2.6, Figure 2.8). Interestingly, the pattern for NDF intake by weight was the reverse of the pattern of NDF intake when measured by calories, which related to the group-specific fiber digestion coefficients used to convert weight intake to caloric intake. Females in GSC group consumed more NDF (g, dry weight) that females in the other two groups, but GSC females consumed fewer calories from NDF than females in other groups.

Some differences in nutrient intake were related to seasonal availability of fruit (Table 2.7, Figure 2.9). When fruit availability was low, females consumed significantly more grams of ADF, ADL and more grams and kcal of NDF. However, seasonal fruit availability had no discernable effect on overall energy (kcal) intake, nor energetic intake from NPE, lipid, protein, TNC, nor dry weight intake of total food or ash.

Visualizing the multidimensional nutritional niche: Diet polygons of the three groups clustered together in nutritional space, indicating similarity in nutrient intake, though there were some slight differences (Figure 2.10). For example, GSC's diet polygon was always positioned

to the left of both GN's and TWS's diet polygons, indicating that mean diet in GSC was lower in relative proportion of protein (Figure 2.10). Some particular foods had a large effect on diet polygon shapes, such as the inclusion of oil palm fruit, which extended TWS's diet polygon along the lipid axis (Figure 2.10a,b).

The RMTs showing the polygons representing the groups' food menus were similar, revealing that individuals in different groups had similar access to nutritional space (Figure 2.11) and groups had broad diets, shown by the spread of the polygons in the possible nutritional space. The nutritional spaces of groups were also similar to one another when calculated using only important foods, though the relative contributions of the foods indicated that subjects achieved this similarity by using different foods to different degrees (Appendix V). When I superimposed the observed mean diets of the three groups onto the food menu polygons, all the groups' mean diets clustered together despite the broad food menu polygons (Figure 2.11). A small exception is shown in Figure 2.11a, where the three groups' mean dietary intakes were positioned in a row along the lipid axis, indicating that groups differed the most in lipid consumption, relative to protein and carbohydrates. Overall, the broad food menus, combined with differences in important foods for groups, but tight clustering of observed diets indicate these monkeys were *food composition generalists* that selected diets that enabled them to be *nutrient intake specialists*.

Expected versus observed diets: RMTs showed that the observed diets of the three groups mostly clustered together and separately from the cluster of expected diets, based on food available to them (Figure 2.12). More specifically, the cluster of observed diets and the cluster of expected diets were spread along the y-axis, indicating that observed diets were higher in relative percentage of lipid than expected diets (Figure 2.12a), but lower in relative percentage of TNC

(Figure 2.12b). When TNC and lipid are combined into one axis, the cluster of observed diets overlaps with, and was positioned similarly to, the cluster of expected diets (Figure 12.2c). When NDF was plotted by itself along the implicit axis (Figure 12.2b-c), expected NDF was generally higher than observed NDF intake for groups. Overall, the clearest pattern indicated that both diet clusters contained similar relative proportions of protein.

Daily path length relationship to group size and fruit availability: The grand mean ± SD DPL was 806 m ± 250 m (range 92-1931, N=371, Table 2.8). The full model including all predictors (percentage of fruit in diet, daily group size, ripe fruit availability, young leaf availability, daily caloric intake, number of GPS counts, monthly rainfall) differed significantly from the null model including only random effects (LRT: X^2(df=7)=47.9, p=3.8e-08). The fixed effects accounted for 13% of the variance and random effects (group, individual ID) accounted for 7% of the variance (indicated by pseudo-R^2 [Lefcheck, 2016]). Percentage of fruit in diet (by kcal) significantly predicted DPL (Table 2.9). When all other predictors were held constant, a one percent increase in fruit in the diet predicted a decrease in DPL by the focal subject of 1.3 m (Table 2.9, Figure 2.13). Group size, ripe fruit availability, young leaf availability and daily caloric intake did not have a significant effect on DPL (Table 2.9).

DISCUSSION

Diet composition by time versus calories

For decades, studies of primate diets used percentage of time spent feeding on various food item types as the primary measure. More recently, however, there has been growing awareness that assessing diets based on measures of time reflects feeding effort better than it measures food mass, energy, or nutrient intake [Aristizabal et al., 2017; Nakagawa, 2009;

Reynoso-Cruz et al., 2016; Rothman et al., 2012]. In this study, both time-based and calorie-based estimates of diet composition, based upon food item types, agreed in identifying the top three food item types (fruit, young leaves, and mature leaves). However, the rank of food types may change depending on how intake is calculated. A study on black howler monkeys compared time-based versus dry weight-based intakes of food and found that when based on time, the diet was majority leaves (65%), with fruit following with less than half that percentage (24%), whereas when the diet was calculated based upon dry weight, fruits were predominant at 53% and leaves followed at 44% [Aristizabal et al., 2017]. Since fruits are generally more nutrient dense than leaves, time-based estimates of diets may underestimate the caloric and nutritional contribution of fruit in the diet. Whether time-based estimates of diet reflects the caloric- or weight-based estimates of diet depends on the intake rate of the food types, the nutritional value of the foods, and the degree to which types are consumed.

While the top food types in the blue monkey diet were consistent regardless of calculation method, there were rank changes for the other categories. Most striking, blue monkeys spent a disproportionate amount of time feeding upon insects, though they contributed only 0.9% of total calories. While insects were relatively high in fat (10 -29%), it may not be energetic gains that drove insect consumption. Besides providing calories, insects provide essential amino acids, vitamins and minerals (notably B12; [National Research Council, 2003; Rothman et al., 2014]). Ash value of insects, a crude measure of minerals, ranged from 3-23% (Appendix I). While blue monkeys may invest the majority of foraging effort on fruit, young leaves, and mature leaves for energetic gain, they also invest considerable time foraging for insects that may provide important amino acids or micronutrients.

Important foods items: Blue monkeys fed from a menu of 445 food items, and only 30 (6.8%) were important to the diet, contributing >1% of calories consumed by females in a group over the study period. Many of the items were important to females in multiple groups: females in all three groups shared 3 important foods and those in two groups shared 11. Most of the important items were fruits and young leaves. Others included three species of gum, one species of flower, one species of bark, and one human-derived food, *ugali.* Gum and *ugali* contained a high percentage of TNC and they represented energy dense foods, so their inclusion was not surprising. The flower came from the species *Zanthoxylum gilleti*, which was also an important source of young leaves and gum. This species was also used for its fruit, leaf buds, and stems, though these items did not contribute more than 1% of total calories (i.e. not "important" food items). Overall, this species may be an important tree for blue monkeys and it ranked as the 17th species upon which females spent the most time feeding (2% of the total time spent feeding, Appendix III). Of the important foods, the inclusion of *Prunus africana* bark was surprising. While blue monkeys do feed upon bark, this behavior is rare (Takahashi pers. obs.). *P. africana* bark had a high fiber percentage (72%, Appendix I) so it seemed unlikely that it was eaten for its nutritional value. More likely, observers mislabeled the behavior of subjects that were high in the tall *P. africana* trees. It may be that blue monkeys used their teeth to tear off bark in search of insects underneath. Alternatively, subjects may have been feeding upon exudate from the tree, though nutritionally, *P. africana* gum was relatively low in TNC (17.6% TNC, mean TNC=51.7 ± SD 35.0 % TNC, N=8 species-specific exudates; Appendix I). Feeding on *P. africana* bark was likely a combination of insect foraging, exudate consumption, and bark consumption.

Diet and food availability: The top two dietary constituents, fruit and young leaf, were predicted by changes in food availability in the environment, though in opposite ways. Young

leaf consumption, by calories, was negatively related to its availability as well as fruit availability, whereas fruit consumption, by calories and percentage of the diet, was positively related to its availability. Since both measures of fruit in the diet were positively related to its availability, blue monkeys both concentrated their diet on fruit and increased the absolute amount of fruit eaten when it was more available. Fruit, especially ripe fruit, is a preferred food item type of blue monkeys (i.e. representation of fruit in diet was greater than expected based on availability [Foerster et al., 2012]) and agonism between females – often a part of competitive interactions – occurred more frequently than expected and disproportionately more when females were feeding on fruit rather than young leaves or insects [Cords, 2000; Pazol & Cords, 2005]. Also, higher ranking females have preferential access to fruits [Foerster et al., 2012]. The study results and the patterns of agonism and priority of access to fruit by higher-ranking females suggest that blue monkeys seek fruit and eat more of it when available. In contrast, they eat fewer young leaves when preferred fruit is less available, suggesting that young leaves serve as fallback food [Marshall et al., 2009]. However, other studies on this study population showed contradictory results for the relationship between diet and food availability. Pazol and Cords [2005] found that on a monthly basis, time spent feeding on plant reproductive parts (fruits and flowers) did not relate to their availability. Similarly, Foerster and colleagues [2012] found that monthly group averages of time spent feeding on fruit did not relate to ripe fruit availability, while time spent feeding on young leaves related significantly and positively to their availability. Differences in methods may explain differences in the findings of these previous studies. Specifically, Pazol and Cords [2005] used a semi-qualitative assessment of overall fruit and flowers (categories of "no", "some" or "many" food items available) while Foerster and colleagues [2012], as well as this study, used semi-quantitative assessments of ripe fruit and

fruit. Also, Pazol and Cords [2005] and Foerster et al. [2012] used different time-based measurements of the diet (percentage of feeding time and percentage of total observation time, respectively) while this study used calorie-based measurements. Future studies with a more nuanced approach, using species-specific scores of food consumption and availability, are needed to disentangle how diet and food availability are related to one another on a species level. It may be that the phenology of certain important food species determines the seemingly contradictory patterns.

Selection ratios of major fruits and young leaves: Ficus lutea had the highest mean selection ratio for both fruit and young leaf. Additionally, its selection ratio for fruit was fifty-seven times greater than the next highest score and it was seventeen times higher than the next score for young leaves. These high values may be explained by the scarce distribution of *F. lutea* throughout the study area, occurring in only 0.06% of transects measured in the near-natural forest and not occurring in transects in the farm/plantation forest (Table 4.1). Its rarity led to very high selection ratios when monkeys fed upon its fruit and young leaves. Other species also had high selection ratios (twelve fruit species and six young leave species had values >5). These high values suggested that subjects targeted these species for consumption, regardless of other fruit or young leaves available. A qualitative comparison with selection ratios reported in an earlier study (differences in methods preclude a quantitative comparison) showed that some species of food trees remained highly selected in the diets of Kakamega blue monkeys over decades, specifically *Antiaris toxicara, Morus lactea, Ficus exasperata*, *Bequaertiodendron oblanceolatum*, *Croton macrostachyus*, *Teclea nobilis* and *Albizia gummifera* [Cords, 1987]. Another study, on a South African population of *C. mitis*, included monthly selection ratios for preferred foods (though computed differently), and reported that *Olea capensis* and *Ficus*

natalensis had some of the highest scores in months when they were available [Lawes et al., 1990]. All three studies reported that *C. mitis* diets included important foods spanning a wide range of selection ratios (from very highly selected to under selected), as well as some shared plant genera (*Croton sp.*, *Ficus sp.)* that were selected despite differences in spatiotemporal distribution and methods.

The majority of fruits with selection ratios >5 were also important food items, again suggesting targeted consumption on a regular basis, so that they contributed significant calories to the diet. By contrast, young leaves with selection ratios >5 were not important food items, except *Teclea nobilis*; it seems that the important young leaf species were so abundant that they were eaten in proportion to their availability, or even less often (e.g. *Zanthoxylum gilletii* young leaves contributed 1.3% of calories to diet of females in GSC, but its mean selection ratio was 0.4). Since fruit was the biggest constituent of the diet, blue monkeys may have selected desirable fruits even if not readily available and thus some fruits were both highly selected and important contributors of calories. Other fruit, like *Bischofia javanica* fruit, were probably so numerous that even though important and heavily consumed, they were eaten in proportion to their availability. Important young leaves, in contrast, were most likely supplemental to fruit and females ate them in proportion their availability, or even less often (i.e. relied on them as a consistent food source), resulting in low selection ratios and demonstrating that species with low selection ratios can still be important in the diet. The overall picture, taking into account identity of important foods and selection ratios, showed that subjects selected specific fruits that were also important to the diet and relied on young leaves that were eaten when available.

Nutrient and energy intake, differences and similarities among groups and across season: Female blue monkeys, regardless of fruit availability or group membership had similar

daily intakes of energy (kcal), non-protein energy (kcal) and protein (kcal). Other parameters (lipid intake (kcal), structural carbohydrate intake (NDF (kcal and g), ADF (g), and ADL (g), total food intake (g), non-structural carbohydrate intake (kcal)), differed by group. Structural carbohydrate intake (NDF (kcal and g), ADF (g), and ADL (g)) was higher when fruit availability was low, compared to when fruit availability was high. These results suggest that female blue monkeys in Kakamega Forest followed a feeding strategy that maintained a mean daily consumption of 126 kcal of protein and 643 kcal of energy, but allowed the other parameters to fluctuate, as reported in other primates (e.g., spider monkeys (*Ateles chamek,* [Felton et al., 2009]), black howled monkeys (*Aloutta pigra*, [Martínez-Mota et al., 2016], and sportive lemurs (*Lepilemur leucopus*, [Dröscher et al., 2016]). Although it appeared that blue monkeys maintained a consistent daily intake of overall energy and of protein, the amounts of energy derived from lipids, fiber fermentation and non-structural carbohydrates (sugars) varied. Similarly, howler monkeys (*Aloutta pigra*) used lipids and sugars interchangeably across seasons to meet their energetic needs [Righini et al., 2017]. Seasonal differences in energy and nutrient intake have also been documented in Verreaux's sifakas (*Propithecus verreauxi*, [Koch et al., 2017]), gorillas (*Gorilla beringei*, [Rothman et al., 2008]), and diademed sifakas (*Propithecus diadema,* [Irwin et al., 2015]).

The pattern of fiber consumption highlighted the important role of assessing fiber digestibility. Females in GSC group consumed significantly more daily grams of NDF than females in the other two groups, but GSC females derived significantly fewer calories from fiber fermentation than their counterparts in other groups, reflecting the fact that females in GSC were considerably less efficient than females in other groups in fermenting. GSC females extracted, per gram dry weight of fiber, a little more than half as many calories as females in other groups.

Thus even though females in GSC consumed more fiber, still their digestive systems extracted less energy. In two wild primate species, Conklin-Brittain et al. [2006] similarly found that using species-specific coefficients to determine energy gain from fiber fermentation significantly changed the estimates of overall daily energy intake. Whereas that study highlighted species differences of fiber digestibility, this study showed that differences can exist between groups in a single population.

There are a few possible explanations for the differences in fiber intake and digestion among females in different groups. Regarding the difference in NDF consumption by weight, it might be that females in GSC group simply ate more fiber-rich fruit. Specifically, females in GSC derived more than half their calories over the study period from two species of fruit (*Bischofia javanica* and *Psidium guajava*). Both fruits had relatively high percentages of NDF (*B. javanica*=57%, *P. guajava*=41% (unripe) or 54 % (ripe). While females in the other two groups also ate these fruits, the fruits did not represent nearly as much of the diet. Thus, it is possible that these two foods in particular contributed to the high level of NDF (g) in diets of females in GSC. Differences in the efficiency of fiber digestion among groups may relate to gut passage rates. When an organism consumes larger amounts of food, the greater food intake is expected to speed the gut passage rate, which in turn would lower fiber digestibility by allowing less time for microbial fermentation of fiber [Conklin-Brittain et al., 2006]. Alternatively, gut passage rate may be affected by the fiber concentration in the diet. When chimpanzees (*Pan troglodytes*) were fed two diets, one high and one low in fiber, the increase in fiber concentration decreased gut passage time and also decreased the digestibility of the fiber content [Milton & Demment, 1988]. Since females in GSC group consumed both higher amounts of food (g) and higher amounts of NDF, either or both explanations may account for their lower fiber

digestibility. Captive blue monkeys, when fed diets containing small plastic markers, showed a mean retention time of food of 20.6 hr [Lambert, 2002]. However, the first marker appeared after only 13 hours and the last marker appeared at the 71.5 hour. The wide range of marker transit times indicates that blue monkeys experience relatively short or long gut passage times. Further studies documenting the variation in diet (both total food amount and proportion of fiber in diet), food passage rate, and fiber digestibility will be needed to identify the factor driving variable fiber digestibility in blue monkeys.

Multidimensional nutritional niche: Female blue monkeys appear to be food composition generalists and nutrient intake specialists. They fed flexibly from a wide menu of 445 possible food items that gave them access to almost all possible nutritional space, except for a small portion of space that would represent foods that were almost entirely protein (Figure 2.11). Despite access to such a wide range of possible nutrient intakes, blue monkeys were actively selective feeders. Females across groups converged on diet compositions of food item types that were remarkably similar when calculated either by time or energy (Figure 2.4). Also, they consumed diets that clustered tightly in nutritional space and also differed from expected diets based upon food availability (Figures 2.10-12). Females in different groups and facing different food availabilities consumed similar amounts of daily energy and protein (Table 2.7). All three RMTs figures, together with the facts important foods varied in type and use among groups, clearly illustrated that females did not randomly consume food, but instead selected specific foods that allowed them to actively regulate and converge on similar nutrient intakes (Figure 2.10-12). Finally, the nutritional balance of the diet consumed by blue monkeys in Kakamega, Kenya was similar to the balance of blue monkeys and other guenons in Kibale Forest, Uganda. When compared to another RMT illustration of primate diets (Figure 2.14), the population mean

diet of Kakamega blue monkeys aligned close to the same TNC:protein ratio radial observed for diets of blue monkeys, red-tailed monkeys, and mangabeys in Kibale, Uganda [Conklin-Brittain et al., 1998a; Raubenheimer et al., 2014; Rothman et al., 2007], though the relative percentage of NDF for Kakamega blue monkey diet was lower. Overall, the nutrient intake composition varied little among females in different groups, across different fruit availability, and in comparison to other guenon populations. Blue monkeys are food composition generalists that feed flexibly from a wide menu to be nutrient intake specialists that actively regulate intake.

Few data exist for other primates but it appears that food composition generalism and nutrient intake specialization may be characteristic of the order. Field observations, combined with an RMT visualization of nutrient intake composition, showed that gorillas (*Gorilla beringei*) are also food composition generalists and nutrient intake specialists that actively regulate nutrient intake [Machovsky-Capuska et al., 2016; Raubenheimer et al., 2014; Rothman et al., 2007]. Chacma baboons (*Papio ursinus*) are nutrient intake specialists in a single dimension (intake was restricted in variation along the protein axis [Johnson et al., 2013; Machovsky-Capuska et al., 2016]) and since chacma baboons are omnivorous [Hamilton et al., 1978], they are most likely food composition generalists as well. Future studies using the multidimensional nutritional niche should focus on primates covering a wide spectrum of diets (i.e. insectivory, gumnivory) and ecological conditions so that researchers can assess whether the combination of food composition generalist and nutrient intake specialization is in fact a characteristic feature of primates.

Comparison with previous data from Kakamega blue monkeys: Dietary data over the years indicated that dietary breadth remained wide, with many foods remaining prominent in the diet over decades. The earliest documentation of the Kakamega blue monkey diet comes from

Cords [1986] using data from 1980-1981. Cords recorded 104 identified plant species in the diet. In this study, I documented a similar number (128) of plant species and morphotypes (Appendix III). While my records included only one instance of vertebrate predation, chicken egg, vertebrate predation is not uncommon (birds [Cordeiro, 1994], mice [Wahome et al., 1988], bats [Tapanes et al., 2016], wild bird eggs, snakes, lizards, squirrels; Cords and Takahashi unpub.). Of the 104 identified plant species reported in 1987, 85% overlapped with the 2015 diet (Appendix III, Table 2.10). In 1980-1981, the top 33 food species (scored by percent frequency of use, N=8454 records, each of the 33 accounted for >0.50 % of frequency of use) overlapped with the 2015 diet. Many of the 1980-1981 frequent foods were also frequent in the 2015 diet, though some foods shifted in relative frequency and new species appeared in the 2015 diet. For example, *Teclea nobilis* was the most frequently consumed food in 1980-1981 (8.05% of feeding observations), but dropped to position 32 in the 2015 diet (0.78% of total feeding time). By contrast, *Bischofia javanica* was listed in the 1980-1981 diet in the 9th position (3.8% of feeding observations) but it jumped to the first position in the 2015 diet at 10.3% of total feeding time, which was a ca. three fold increase from 1980-1981. Finally, most of the 1980-1981-documented species that were not observed in the 2015 diet were minor contributors to the annual diet (<0.06% of feeding observations). However, less frequent foods are less likely to be detected and thus our study may have failed to document their use.

The major changes observed between the 1980-1981 diet and 2015 diet likely resulted from two main factors. First, the study population was not well habituated in 1980-1981 and monkeys rarely came to the ground, making it less likely that Cords would have observed them consuming low-lying herbaceous shrubs such as *L. camara* and *R. rigidus*. Second, in the 1980s, blue monkeys from TWS and GN groups did not range in the village forest or farm/plantation

forests (Cords, pers. comm.). Since then, they have moved into these areas and, indeed, subjects used these habitats almost daily. As a result, they gained access to new foods that became a common component of their diet (e.g. *Psidium guajava* and *Cupressus lusitanica* together represented a tenth of all feeding time). The 1980-1981 to 2015 diet comparison demonstrated that blue monkeys maintained a broad diet and adjusted their diet to capitalize on new foods as they expanded into new habitats, again emphasizing their dietary flexibility.

Finally, I compared diet compositions (based on time spent on larger categories) of Kakamega blue monkeys using data at approximately 20 year intervals [Cords, 1986, 1987; Pazol & Cords, 2005]. Differences in behavioral sampling methods preclude detailed comparison, though the time spent feeding (as percentage of total time observed) was similar between this study (29%) and 1997-1998 (33%). Unsurprisingly, across the studies and despite differences in methods, fruit emerged as the main constituent of the diet (Figure 2.15). A key difference in methods was that the previous studies defined feeding behavior to include foraging while this study did not. That difference most likely explains the most obvious dissimilarity, the estimate for insects (4.9,16.8, and 24%, [Cords, 1986; Pazol & Cords, 2005]). Specifically, the higher percentages in Pazol and Cords [2005] and Cords [1986] include foraging for insects, a time-intensive activity. Also, there was more than a third difference in percentage of time feeding on young leaves between the earliest and this study. As mentioned earlier, monkeys in the 1980-1981 were not as habituated, so they were less likely to be lower to the ground where they could consume young leaves from herbs and small trees. Overall, though, the comparison confirmed that over the years, female blue monkeys in Kakamega Forest changed little in the amounts of time they spent feeding upon various food item types. They devoted the majority of their feeding time to fruits, young leaves, and insects.

Comparison of Kakamega diet to other blue monkey populations and guenons: Only one other study [Conklin-Brittain et al., 1998b] has analyzed the nutritional composition of the blue monkey diet, focusing on two groups in Kibale Forest, Uganda studied over a period of 11 months. The two groups consumed mean diets that were very similar in composition (lipid: 4% and 3%; crude protein: 18% and 16%; TNC: 35% and 38%; NDF: 32% and 33%; ADF: 20% and 20%). In contrast, the mean diet for Kakamega blue monkeys was higher in lipids (7%), lower in protein (15%), lower in TNC (30%), and higher in structural carbohydrates (NDF: 41%, ADF: 33%). However, Conklin-Brittain and colleagues reported crude protein while the percentage reported in this study was for available protein. Thus, it is likely that available protein percentages in the diets of the two populations are very similar, which agrees with the overall picture that blue monkeys appear consistently to consume the same amount of protein on a daily basis, allowing other macronutrient intakes to vary.

Coleman and Hill [2014a] provided a detailed summary of diet composition of different populations of *C. mitis* (studies lasting >6 months). Chapman and colleagues [2002] also compiled diet compositions of 25 populations of this species and other cercopithecines. These comparisons highlight that *C. mitis* diets are quite variable in almost all food item types among populations (Table 2.11). For example, some reports indicate that fruit constituted as much as 91% of the diet [Lawes et al., 1990], though there are also reports of populations eating very little fruit, with fruit contributing as little as 17% of feeding time [Tesfaye et al., 2013]. This large variation is also characteristic of guenon diets in general [Chapman et al., 2002]. The NRC reported large ranges in all food categories: twenty-fold range of variation in percentage of fruits, almost a hundred-fold range for leaves and anywhere from zero to thirty-fifty percent for other food categories [National Research Council, 2003]. These wide ranges indicate that categorizing

blue monkeys, and guenons more generally, as "frugivorous" may mask much of the variation seen in the diets of different subpopulations, populations and species [Chapman et al., 2002; Struhsaker, 2017]. Blue monkeys had the widest range in variation in some food item types when compared to other guenons [Chapman et al., 2002]. Chapman et al. [2002] reported coefficients of variation (CV) for variability in percentage of dietary components among populations of same species and blue monkeys had the highest CV for the fruit category and second highest CV for insects. These CVs were later reinforced by Coleman and Hill's [2014a] report that *C. mitis* diet varied across a latitudinal gradient of population location (data from 14 populations spanning as far south as Ngoye Forest, South Africa (28^{o} 50' S, 31 ^{o}42'E) and as far north as Jibat Forest, Ethiopia (8 ^{o}43' N, 37 ^{o}33' E). Populations closer to South Africa consumed relatively more insects and less fruit while populations closer to Ethiopia consumed relatively more fruit and fewer insects. More accurately, these monkeys should be considered food composition generalists, able to consume a range of diet compositions.

Daily path length: The range of DPLs in the population was very large, from 92 m to 1931 m, a ca. twenty-fold difference. Other studies of DPL (based on *group* movements, except Irwin [2008] who measured individual movements) also reported a wide range, but none as large in magnitude as seen in Kakamega blue monkeys (e.g., *Propithecus diadema*: 342-2014 m [Irwin, 2008], *Papio ursinus*: 2-7 km [Hoffman & O'Riain, 2012], *Nomascus concolor jingdongensis*: 300-3144 m [Fan & Jiang, 2008], *Papio hamadryas hamadryas*: 3-11 km [Swedell, 2002]). Some populations had a relatively small range of DPLs (*Trachypithecus leucopcephalus* 450-536 m [Huang et al., 2017]). Even compared to other populations of blue monkeys, the range I observed was bigger (*C. mitis bourtourlinii*, range 350-1612 m (based on group movements [Tesfaye et al., 2013]).

Coleman and Hill [2014a] reported group day journey length from 6 studies of blue monkeys [Butynski, 1990; Coleman, 2013; Coleman & Hill, 2014b; Cords, 1986, 1987; Kaplin et al., 1998; Kaplin, 2001; Tesfaye et al., 2013]. The DPL (m) for these 6 studies ranged from 799 m to 1,906 m. The mean individual DPL for the Kakamega population, as calculated in this study, was 805 ± SD 265 m (N=371), i.e. relatively low compared to these other studies. It was also 33% lower (on average) than previously reports from the 1980s from the same study population [Cords, 1986, 1987], though closer to DPLs from 2012 (range of median group DPL: 583-733 m [Cords, 2012]). It may be that the spatial distribution of food and changing ranging patterns of groups explained the decrease in DPL from 1980s to 2010s. Since the 1980's, groups in the study population began to use different habitats, namely the village forest and farm/plantation forests. The use of food resources in these habitats might have reduced the amount of travel needed to reach food resources and thus might explain the reduced DPL observed relative to values from the 1980s. The DPLs measured in 2012, which were shorter than those I measured, might be explained by methodological differences. In 1980 and 2012, Cords calculated DPL using hourly locations of a group's "center of mass" [Cords, 2012], whereas my DPLs were calculated on half-hour locations of individual movements. The more frequently measured locations meant a more fine-grained calculation of DPL that would account for more of the windings along the travel pathway. Sennhenn-Reulen et al. [2017] showed that DPLs (of Guinea baboons, *Papio papio)* based on hourly versus half-hourly locations varied considerably, both to one another and to more continuous DPLs based on approximately 1 minute locations. Also, DPLs based on group movements do not account for circuitous movements of individuals within the group, so it is not surprising that the group DPLs from 2012

were shorter than DPLs based on individual movements as measured in this study. It may be this difference in DPL reflects differences in methods and not true DPL differences.

DPL changed with the percentage of fruit in diet and monthly rainfall (Table 2.9). Blue monkeys traveled less when their diet included a higher percentage of fruit. This pattern might be explained by the phenology of important fruiting trees. Trees such as *Ficus spp., Antiaris toxicara, Maesopsis eminii* and *Bischofia javanica* produce vast crops of fruit. When these important fruits were in season, females spent lots of time in these trees, sometimes returning to a particular tree repeatedly during the day, and reducing travel accordingly. Travel also decreased during months with heavy rains. Heavy rains coincided with decreased temperature, so females were more stationary and huddled together for thermoregulation.

It is worth noting that daily group size was not significantly related to DPL, confirming a previous report on individual DPL by Cords [2012]. This study's results also agreed with findings from an another population of blue monkeys in Jibat Forest, Ethiopia, where researchers found no significant relationship between group DPLs and group size [Tesfaye et al., 2013]. Other factors may influence DPL. For example, in Soutpansberg Mountains, South Africa, researchers found that range use by samango monkeys was not correlated to resource distribution, but instead to predation risk from eagles [Coleman & Hill, 2014b]. Overall, studies of DPL in blue monkeys conform to Isbell's [1991] conclusion that guenons do not show a relationship between DPL and group size. The lack of relationship suggests that intragroup scramble competition over food is relatively weak, and females within a group may avoid competition by spreading out when foraging.

In summary, blue monkeys are a generalist species, able to persist in a variety of ecological conditions via a dietary strategy of omnivory. They feed flexibly, which results in

variable diet. Blue monkeys should be classified more precisely as food composition generalists and nutrient intake specialists. Comparisons between groups at one time, across the population at different times, and between populations support this conclusion. The wide variation observed in the blue monkey diet supports the growing realization that categorizing a species by its most common diet constituent (e.g. frugivore) is overly simplistic and such broad labels mask much of the variation that may be characteristic of a species. Blue monkeys, while preferring fruit, also persist on diets focused on leaves. Their ability as a species to display such feeding flexibility may be an explanation for their widespread geographic distribution in Africa and their ability to survive in degraded or human-modified habitats [Mammides et al., 2009; Fashing et al., 2012; Lawes et al., 2013; Chap 4].

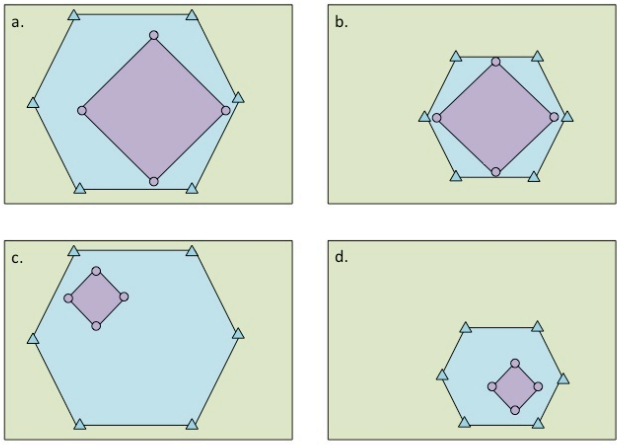


Figure 2.1. The multidimensional nutritional niche. The multidimensional nutritional niche defines the diet of an organism on multiple levels. When an organism navigates the food environment (green/grey background), it selects food items (blue triangles) that define its diet on the level of food composition (blue polygon). Its food choices determine nutrient intake (purple circles). Each level may span the generalist-specialist spectrum. For example in a) if an organism consumes food items that vary widely in nutritional composition and tolerates nutrient intake that also varies widely, then that organism is a food composition generalist and nutrient intake composition generalist. In contrast, d) illustrates when an organism consumes food items that vary relatively little in nutritional composition and also the nutrient intake composition varies relatively little, indicating that the organism is both a food composition specialist and nutrient intake composition specialist. b) shows a food composition specialist and nutrient intake composition generalist and c) shows a food composition generalist and a nutrient intake composition specialist. Few studies exist for the multidimensional nutrition niche, but see data on gorillas (*Gorilla beringei*, [Machovsky-Capuska et al., 2016]) and wild boars (*Sus scrofa,* [Senior et al., 2016]). Figure represents an adaption from a figure in Machovsky-Capuska et al. [2016].

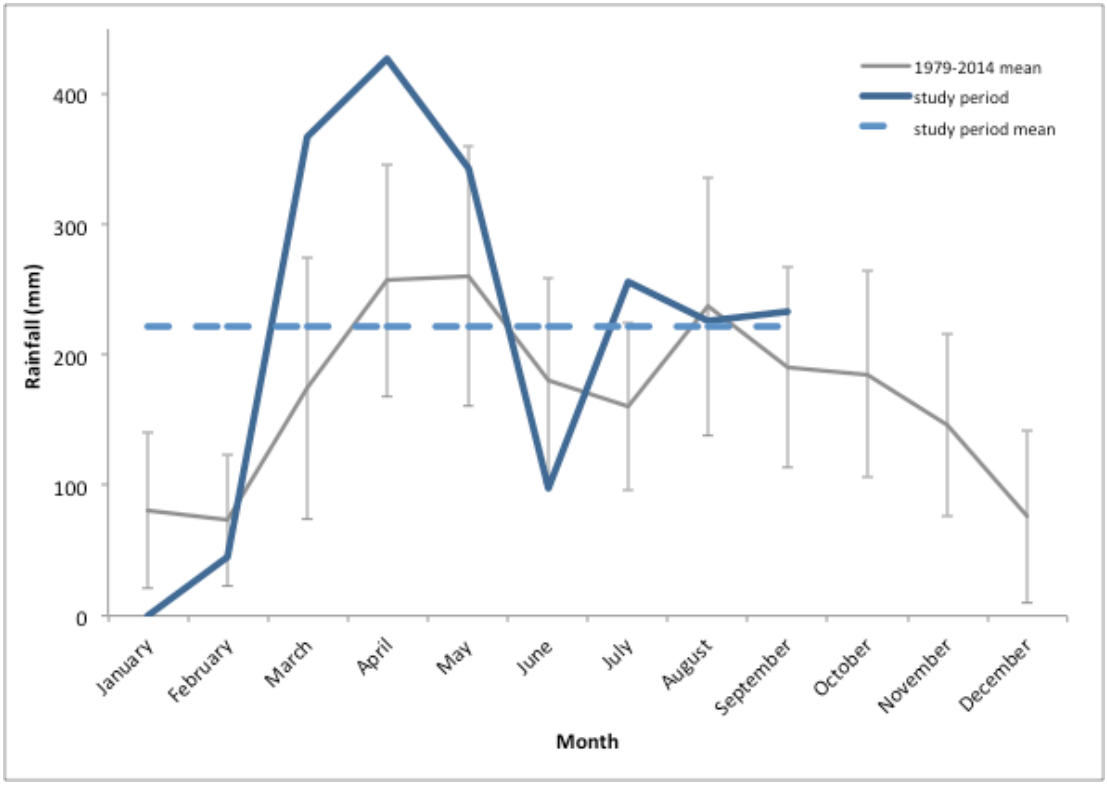


Figure 2.2. Monthly variation in rainfall at study site in Kakamega Forest, Kenya during this study. Longterm rainfall norms are shown in grey (Cords unpub. data), with error bars representing standard deviation.

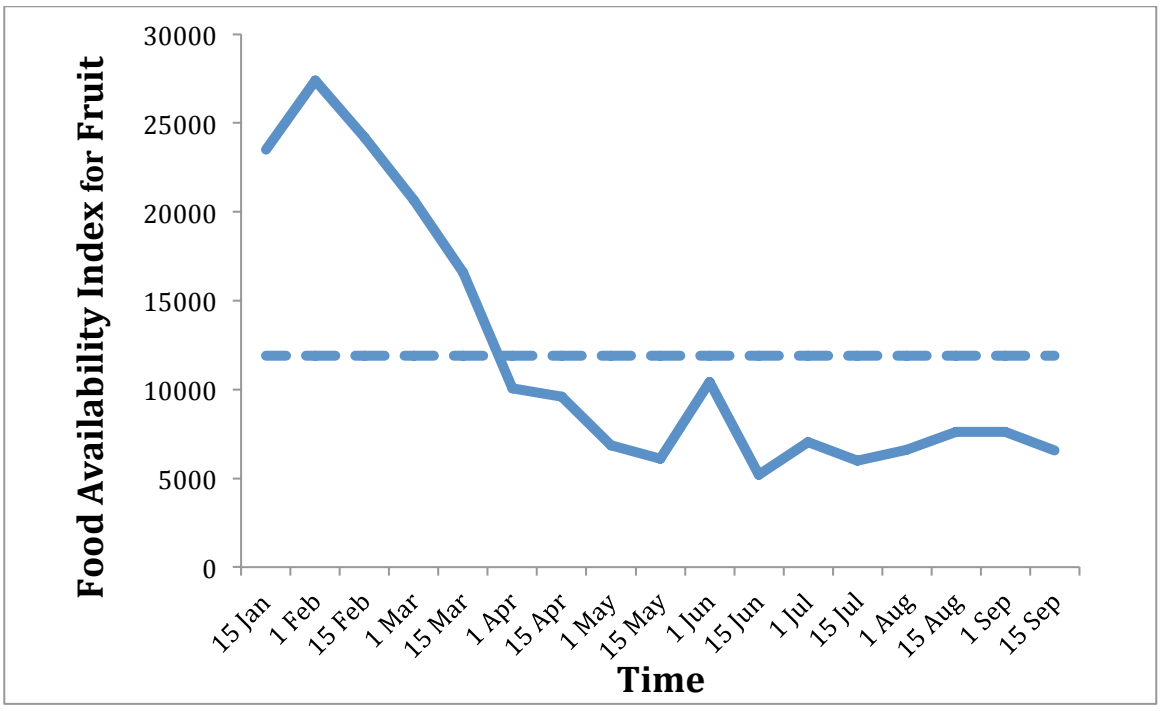


Figure 2.3. Variation in food availability index (FAI) for fruit (dotted line shows mean value, 11885). See Methods for details on calculating FAI fruit. Species contributing to the fruiting peak early in the study included *Acrocarpus fraxinifolius, Antiaris toxicaria*, *Bischofia javanica*, *Bridelia micrantha, Celtis africana, Ficus exasperata, Ficus sansibarica, Ficus sur, Ficus thonningii, Funtumia africana, Harungana madagascariensis, Morus lactea, Polyscias fulva, and Spathodea campanulata*. The timing of the fruiting peak matches that observed in past years ([Foerster et al., 2012], Cords unpub.).

Table 2.1. Vegetation composition of the three habitat types, including basal area of all and top five trees and herbaceous plants ≥ 5 cm DBH in randomly located 10 x 100 m transects. Mean (and SD) basal area (BA, m^2 per ha) was calculated by first summing the basal areas of a species in a single transect, then averaging across transects. % indicates percentage of transects in which each species occurred (i.e. a measure of frequency/distribution). Trees and shrubs ≥ 5 cm DBH in the village forest were measured through a complete inventory of the area used by TWS group and/or GN group and scaled to represent BA cm^2 per ha, like the other habitat types.

Near-natural forest (N=36 transects)				Farm/plantation forest (N=10 transects)				Village forest (full inventory)	
Species	Mean BA (m^2 per ha)	SD	%	Species	Mean BA (m^2 per ha)	SD	%	Species	BA (m^2 per ha)
all species	59.3	28.7		all species	60.6	48.0		all species	13.7
Olea capensis	9.6	16.1	56	*Bischofia javanica*	33.6	49.8	90	*Cupressus lusitanica*	3.4
Zanthoxylum gilletii	5.9	8.6	50	*Psidium guajava*	8.9	7.8	100	*Sapium ellipticum*	1.1
Antiaris toxicaria	5.8	9.8	81	*Grevillea robusta*	5.4	12.9	20	*Maesopsis eminii*	0.9
Funtumia africana	4.7	5.0	89	*Eucalyptus saligna*	2.8	5.4	30	*Khaya anthotheca*	0.8
Prunus africana	4.1	6.0	42	*Cupressus lusitanica*	2.7	7.3	20	*Bischofia javanica*	0.7

Table 2.2. Focal follow summary, showing time (hr) spent feeding, in and out of sight, and follow length. I calculated values by averaging daily values by individual, and subsequently averaging over group and population (i.e. grand means). “Not feeding”=All observed behaviors except feeding. “In sight”=Feeding combined with Not Feeding. “Focal follow length”=Feeding combined with Not feeding and Out of sight. “% Feeding”=Feeding divided by In Sight. “% In Sight”=In Sight divided by Focal follow length. “SD”=standard deviation. N represents subjects.

	GN (N=8)		GSC (N=8)		TWS (N=8)		Population (N=24)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Feeding (hours)	2.7	0.5	2.6	0.4	2.7	0.2	2.7	0.4
Not feeding (hours)	6.4	0.4	6.5	0.4	6.4	0.3	6.4	0.4
Out of sight (hours)	0.8	0.2	0.6	0.1	0.8	0.2	0.7	0.2
Feeding + Not feeding (hours)	9.1	0.2	9.1	0.2	9.1	0.3	9.1	0.2
Out of sight + Feeding + Not feeding (hours)	10.0	0.1	9.7	0.1	9.9	0.2	9.9	0.2
% Feeding	29.6	4.5	28.0	4.1	30.1	2.5	29.2	3.8
% Feeding + Not feeding	91.7	1.5	93.9	1.0	92.0	2.2	92.5	1.9

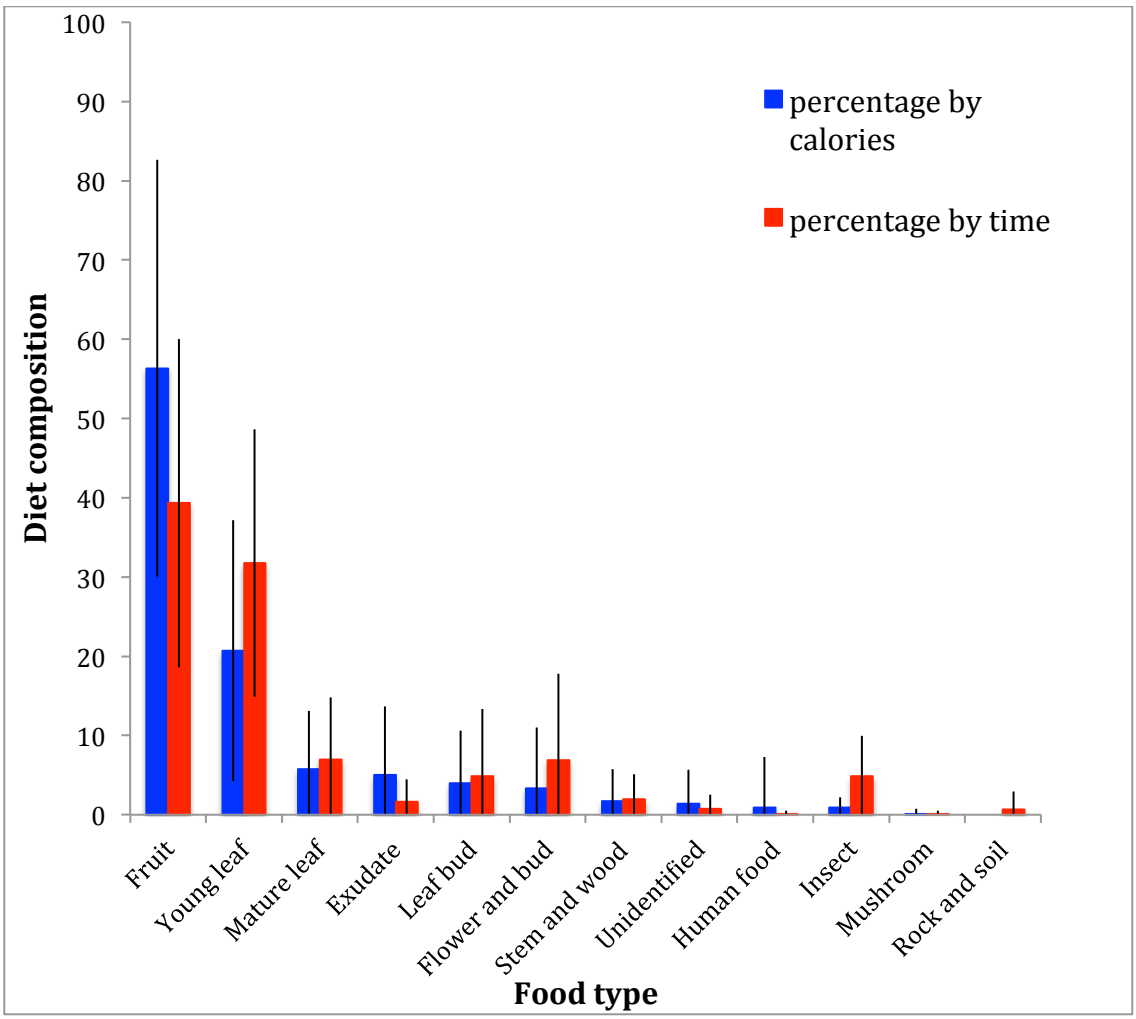
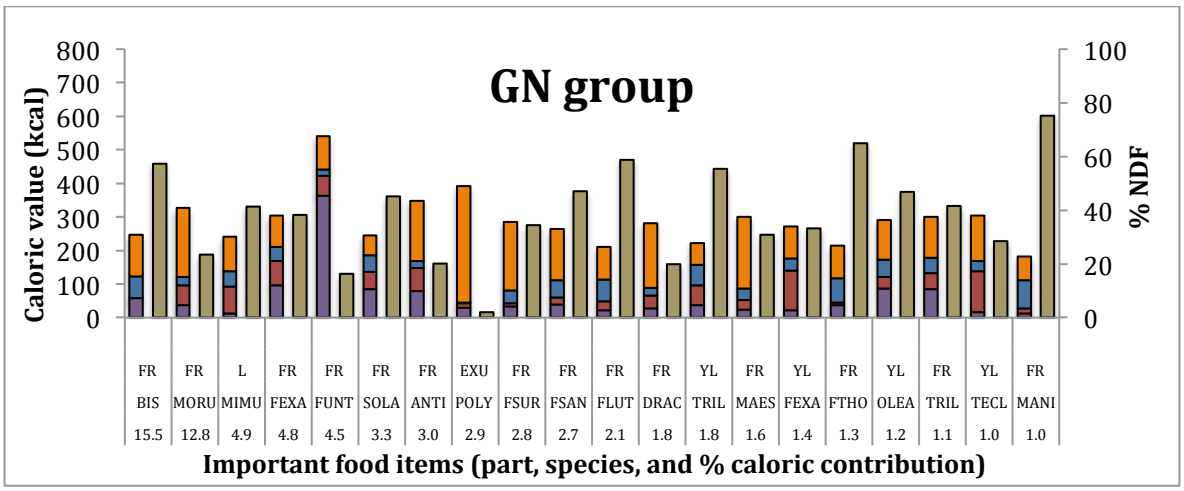
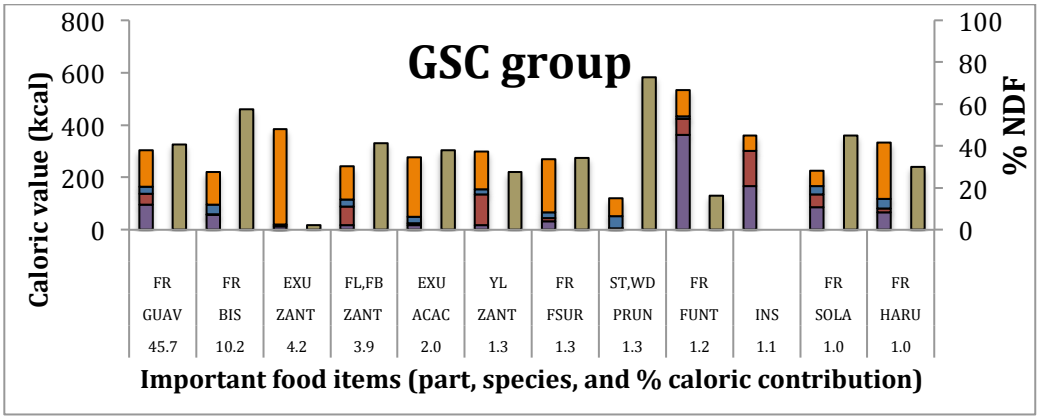


Figure 2.4. Population diet composition by item, expressed in terms of mean % feeding time (blue) and mean % calories ingested (red) across 371 female-days (black lines represent standard deviation). Columns are ordered by descending percentage derived from calories. Since laboratory analyses measured macronutrients only, rock and soil, which may have supplied important minerals, were ranked by time, but not calories.

a.



b.



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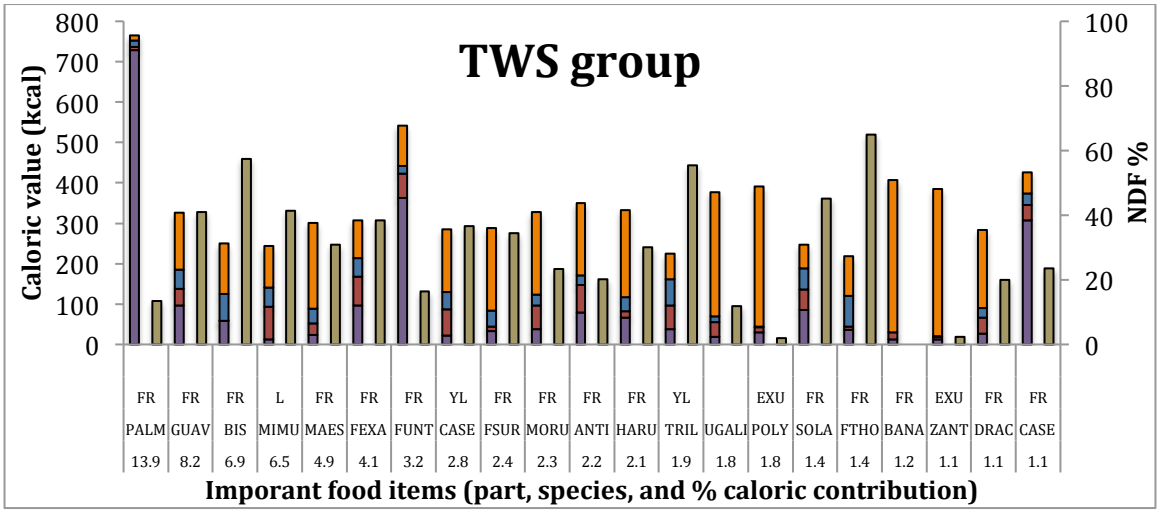


Figure 2.5. Important foods by group. Important foods contributed ≥1% of total calories consumed by females in a group (GN=124 female-days, TWS=124 female-days, GSC=123 female-days). Horizontal axis shows important food items, specifying food part, species, and

percentage contribution to diet. Stacked columns show the contribution of lipid (shown in purple), protein (shown in red), and structural carbohydrates (shown in blue), and non-structural carbohydrates (shown in orange) calories per 100 g of food (dry matter basis). Brown columns show the structural carbohydrate (NDF) percentage. Food part abbreviations are as follows: EXU (exudate), FR (fruit), L (young and mature leaves), ST, WD (stem and wood), YL (young leaves). Species codes are as follows: ACAC (*Acacia abyssinica*), ANTI (*Antiaris toxicaria*), BANA (*Musa paradisiaca*, banana), BIS (*Bischofia javanica*), CASE (*Casearia battiscombei*), DRAC (*Dracaena fragrans*), FEXA (*Ficus exasperate*), FLUT (*Ficus lutea*), FSAN (*Ficus sansibarica*), FSUR (*Ficus sur*), FTHO (*Ficus thonningii*), FUNT (*Funtumia africana*), GUAV (*Psidium guajava*), HARU (*Harungana madagascariensis*), MAES (*Maesopsis eminii*), MANI (*Manilkara butugi*), MIMU (*Mimulopsis solmsii*), MORU (*Morus lactea*), OLEA (*Olea capensis*), PALM (*Elaeis sp*., oil palm), POLY (*Polyscias fulva*), PRUN (*Prunus africana*), SOLA (*Solanum mauritianum*), TECL (*Teclea nobilis*), TRIL (*Trilepisium madagascariense*), ZANT (*Zanthoxylum gilletii*).

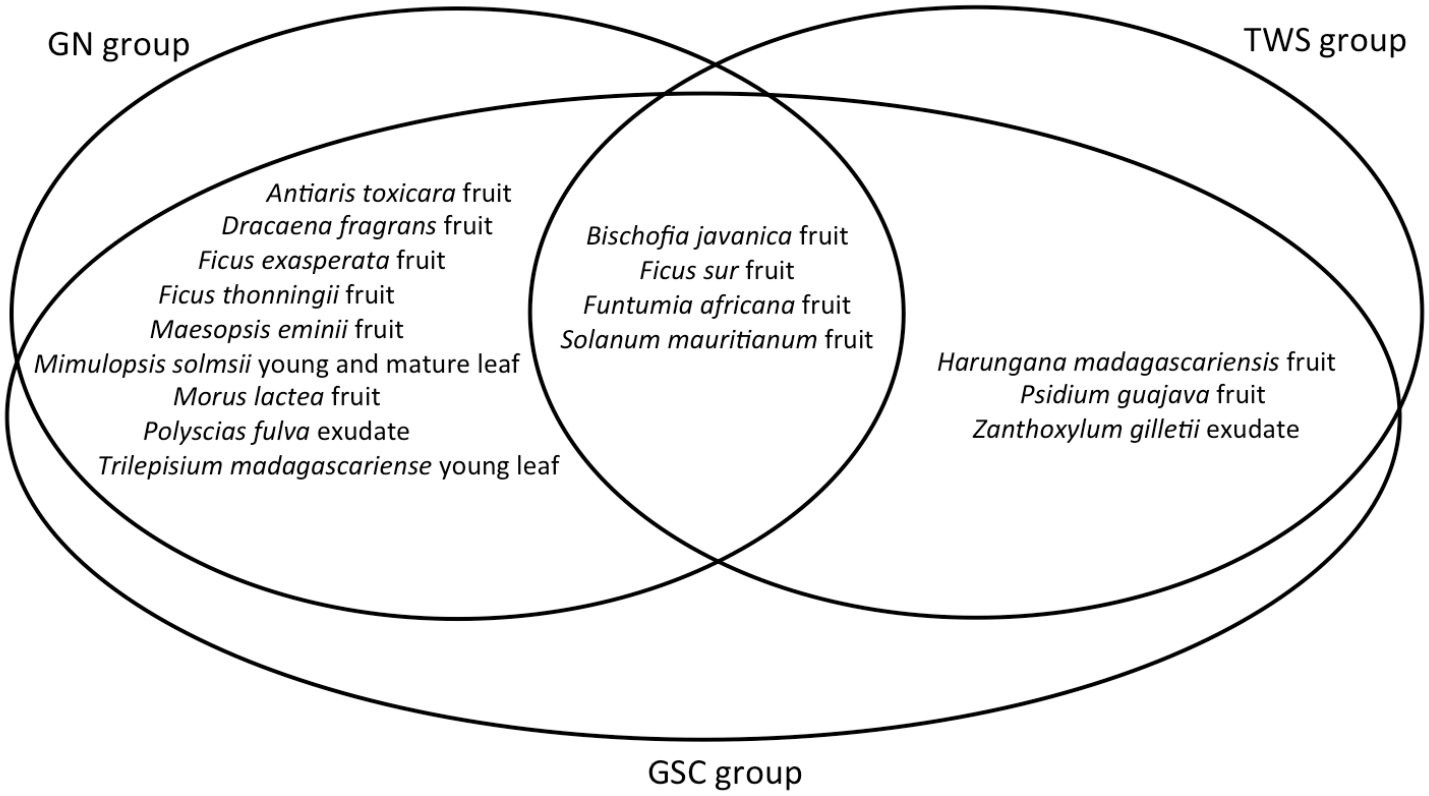


Figure 2.6. Shared important foods by group. Important foods contributed ≥1% of total calories consumed by females in a group (GN=124 female-days, TWS=124 female-days, GSC=123 female-days). Foods listed in upper left were important to both GN and TWS group. Foods listed in upper right were important to both TWS and GSC group. Foods listed on bottom were important to all three groups. No food was uniquely important to both GN and GSC groups. Within each grouping, foods are listed alphabetically.

Table 2.3. Linear mixed models for relationships between diet (% fruit (computed using kcal), absolute amount (kcal) of fruit, absolute amount (kcal) of young leaves) and food availability (N=371 female-days for % fruit, N=371 female-days for fruit (kcal), N=369 female-days for log (young leaves (kcal))). Models included Subject ID nested in Group as random effects. R^2 values are pseudo- R^2 [Lefcheck, 2016]. * indicates significance.

Response variable	Parameters	Estimate	SE	95% CI	DF	T-value	P value	Fixed effects R^2	Random effects R^2
Percentage of fruit in diet (by kcal)	FAI fruit/1000*	1.13	0.17	0.78 − 1.47	43.81	6.48	6.76e-08	0.11	0.01
	Intercept*	43.84	2.46	38.83 − 48.54	6.77	17.84	6.06e-07		
Square root (fruit in diet (kcal))	FAI fruit/1000*	0.24	0.06	0.13 − 0.35	230.07	4.35	2.01e-05	0.05	5.41e-03
	Intercept*	15.33	0.75	13.88 − 16.79	82.51	20.53	<2.00e-16		
Square root (young leaves in diet (kcal))	FAI young leaves/1000*	-0.15	0.04	-0.22 − -0.04	14.14	-3.47	3.71e-.03	0.15	0.11
	FAI fruit/1000*	-0.13	0.03	-0.18 − -0.08	276.30	-4.38	1.70e-05		
	Intercept*	17.07	1.86	12.41 − 20.22	8.59	9.17	1.00e-05		

Table 2.4. Selection ratios for fruit and young leaves of major food species. Selection ratios above 1 indicate positive selection. SD=standard deviation. * indicates species for which there were feeding records, although phenology scoring indicated this food was not available: these instances were excluded from selection ratio means. Species are listed by descending mean.

Fruit selection ratios				Young leaf selection ratios			
Species	Mean	SD	N	Species	Mean	SD	N
*Ficus lutea**	2591.3	5085.8	17	*Ficus lutea*	649.4	824.4	2
*Ficus sur**	45.8	70.9	27	*Croton macrostachyus*	38.6	102.2	10
Elaeis sp., oil palm*	31.6	34.1	7	*Aulacocalyx diervilleoides*	18.6	24.7	147
*Morus lactea**	24.5	16.3	30	*Teclea nobilis*	13.2	15.5	76
Spathodea campanulata	23.6	N/A	1	*Albizia gummifera*	8.0	16.2	70
Solanum mauritianum	13.9	26.9	142	*Ficus sur*	5.6	12.3	49
Psidium guajava	9.2	15.3	158	*Chaetacme aristata*	4.9	5.9	77
*Antiaris toxicaria**	9.0	10.5	13	*Morus lactea*	3.3	5.0	20
Aulacocalyx diervilleoides	6.9	13.5	14	*Ficus exasperata*	2.2	6.9	89
*Ficus exasperata**	6.5	6.6	58	*Acrocarpus fraxinifolius*	2.1	N/A	1
Croton sylvaticus	6.2	7.7	5	*Acacia abyssinica*	2.0	2.1	69
Lantana camara	5.1	6.0	31	*Antiaris toxicaria*	1.6	2.4	30
*Bridelia micrantha**	4.3	5.9	5	*Trilepisium madagascarensis*	1.3	1.9	172
*Croton macrostachyus**	2.0	N/A	1	*Celtis africana*	1.3	1.7	106
*Harungana madagascarensis**	1.8	1.9	37	*Polyscias fulva*	1.1	1.8	11
*Celtis africana**	1.6	2.2	22	*Bischofia javanica*	1.0	1.4	8
*Ficus thonningii**	1.5	1.7	19	*Spathodea campanulata*	0.8	1.7	69
*Maesopsis eminii**	1.1	1.1	48	*Prunus africana*	0.6	0.9	35
Bischofia javanica	1.0	1.5	176	*Olea capensis*	0.5	1.2	102
*Funtumia africana**	0.9	1.4	47	*Bridelia micrantha*	0.5	0.6	2
*Prunus africana**	0.5	0.4	11	*Zanthoxylum gilletii*	0.4	0.5	56
*Olea capensis**	0.3	0.7	8	*Ficus thonningii*	0.2	0.2	87
*Ficus sansibarica**	0.2	0.2	17	*Funtumia africana*	0.0	N/A	1
*Zanthoxylum gilletii**	0.0	0.0	3	*Ficus sansibarica*	0.0	0.0	23
Polyscias fulva	eaten, but not available			*Harungana madagascarensis*	eaten, but not monitored		
Trilepisium madagascarensis	eaten, but not available			*Lantana camara*	eaten, but not monitored		
Acacia abyssinica	not eaten			*Maesopsis eminii*	eaten, but not monitored		
Acrocarpus fraxinifolius	not eaten			*Cordia africana*	not eaten		
Albizia gummifera	not eaten			*Croton sylvaticus*	not eaten		
Chaetacme aristata	not eaten			*Cupressus lusitanica*	not eaten or monitored		
Cordia africana	not eaten			*Elaeis sp.,* oil palm	not eaten or monitored		
Teclea nobilis	not eaten			*Psidium guajava*	not eaten or monitored		
Cupressus lusitanica	not monitored			*Solanum mauritianum*	not eaten or monitored		

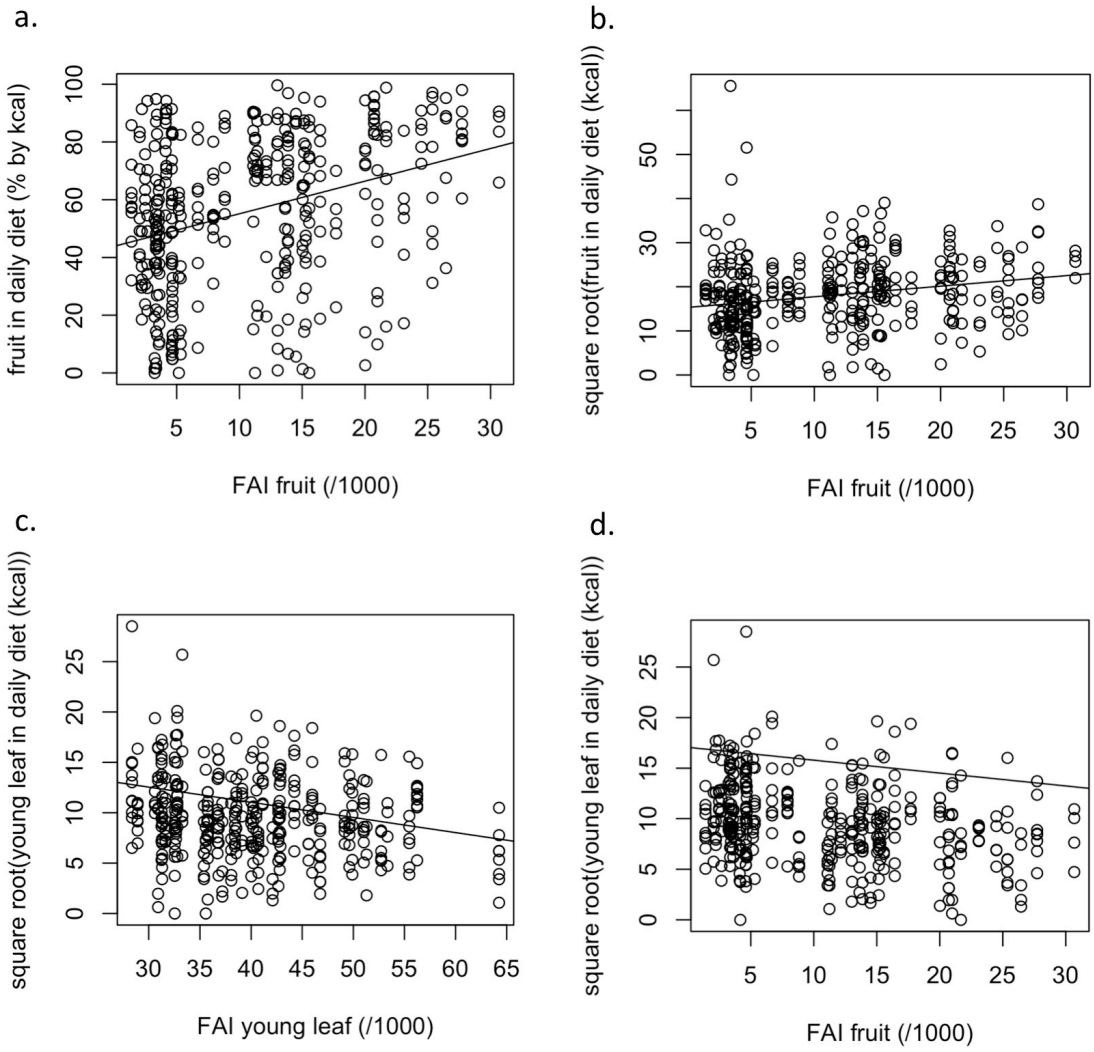


Figure 2.7. Relationships among diet and food availability. Black line shows predicted slope of dependent variable and intercept of linear mixed model. All graphs include 371 female-days. For a) y-axis is percentage of fruit in the diet (by kcal), x-axis is FAI of fruit. For b) y-axis is the square root of amount of fruit in the diet (by kcal), x-axis is FAI of fruit. For c) y-axis is the square root transformation of amount of young leaves in the diet (by kcal), x-axis is FAI of young leaf. For d) y-axis is the square root transformation of amount of young leaves in the diet (by kcal), x-axis is FAI of fruit.

Table 2.5. Daily intake by group and population. Grand means were calculated by first averaging over 15-16 daily intakes of individuals, then across individuals (8 per group). SD indicates standard deviation. N indicates number of individuals. NPE (kcal) is sum of TNC, lipid and NDF. Food (kcal) is sum of NDF, TNC, lipid and protein. Food (g) is sum of NDF, TNC, lipid, protein and ash. Nutritional measures are ordered in descending order by population grand mean by kcal, followed by descending order for ADF, ADL and ash in grams. Grams are on a dry matter basis. Daily intakes were calculated using data from full-day focal follows combined with nutritional value of species-specific food items. Caloric value of NDF was calculated using a group-specific digestion coefficient. See Methods for details.

	GN (N=8)		GSC (N=8)		TWS (N=8)		Population (N=24)	
Nutritional measure	grand mean	SD	grand mean	SD	grand mean	SD	grand mean	SD
Food (kcal)	587.7	88.8	678.4	72.2	645.2	134.5	637.1	104.7
Food (g)	213.5	33.1	259.9	31.1	205.9	28.5	226.4	38.3
NPE (kcal)	481.9	78.5	567.1	68.7	538.7	126.3	529.3	97.3
NPE (g)	169.7	28.4	216.4	28.4	164.1	23.0	183.4	35.0
TNC (kcal)	276.9	42.3	338.4	23.1	264.7	36.6	293.3	46.9
TNC (g)	69.2	10.6	84.6	5.8	66.2	9.2	73.3	11.7
Lipid (kcal)	106.6	21.4	153.2	34.8	183.6	110.1	147.8	72.4
Lipid (g)	11.8	2.4	17.0	3.9	20.4	12.2	16.4	8.0
Protein (kcal)	105.8	12.5	111.3	12.6	106.5	14.4	107.8	12.9
Protein (g)	26.4	3.1	27.8	3.2	26.6	3.6	27.0	3.2
NDF (kcal)	98.4	17.9	75.5	13.0	90.4	14.6	88.1	17.5
NDF (g)	88.7	16.2	114.8	19.7	77.6	12.5	93.7	22.3
ADF (g)	71.1	14.8	93.3	18.1	58.4	10.1	74.3	20.4
ADL (g)	36.8	8.0	42.7	6.9	29.2	5.7	36.3	8.7
Ash (g)	17.4	2.0	15.7	2.0	15.1	2.5	16.1	2.4

Table 2.6. Significant differences in daily intake by females in different groups. Linear mixed models tested differences between all pairs of groups (by adjusting the reference group ID, indicated in parentheses). All models included Subject ID as a random effect and N=371 daily intakes. Only models and pairwise comparisons with significant fixed effects are presented here, ordered by descending fixed effect R^2 value. R^2 values are pseudo- R^2 [Lefcheck, 2016]. * indicates significance.

Response variable	Predictor	Estimate	SE	95% CI	DF	T-value	P value	Fixed effects R^2	Random effects R^2
ADF (g)	Group (GSC)							0.08	0.03
	TWS*	-34.85	7.33	-48.85 – -20.86	20.88	-4.75	1.09E-04		
	GN*	-22.18	7.33	-36.17 – -8.19	20.88	-3.03	6.47E-03		
	Intercept	93.16	5.19	83.33 – 103.08	20.99	17.95	3.26E-14		
NDF (g)	Group (GSC)							0.07	0.02
	TWS*	-37.04	8.17	-52.63 – -21.46	20.88	-4.54	1.82E-04		
	GN*	-26.01	8.17	-41.60 – -10.43	20.88	-3.19	4.47E-03		
	Intercept	114.55	5.78	103.52 – 125.59	21.01	19.81	4.44E-15		
ADL (g)	Group (TWS^A)							0.05	0.02
	GSC*	13.45	3.46	6.84 – 20.06	21.07	3.88	8.53E-04		
	GN*	7.58	3.46	0.98 – 14.18	20.94	2.19	0.04		
	Intercept	29.20	2.44	24.53 – 33.86	20.94	11.95	8.22E-11		
Food (g)	Group (GSC)							0.04	3.52E-04
	TWS*	-53.53	15.50	-83.77 – -23.27	21.09	-3.45	2.37E-03		
	GN*	-46.27	15.50	-76.51 – -16.01	21.09	-2.99	7.03E-03		
	Intercept	259.52	10.98	238.09 – 280.96	21.26	23.64	<2.00E-16		
NDF (kcal)	Group (GSC)							0.03	0.03
	TWS*	22.94	7.66	0.31 – 29.57	21.10	2.99	6.89E-03		
	GN*	20.99	8.03	8.31 – 37.57	21.03	2.61	0.02		
	Intercept	75.37	5.43	65.02 – 85.73	21.22	13.89	3.99E-12		
TNC (kcal)	Group (GSC)							0.03	0
	TWS*	-73.43	22.31	-117.09 – -29.77	368.90	-3.29	1.09E-03		
	GN*	-61.64	22.31	-105. 30 – -17.98	368.90	-2.76	6.01E-03		
	Intercept	338.16	15.81	307.23 – 369.10	368.90	21.40	<2.00E-16		
Lipid (kcal)	Group (TWS^A)							0.01	0
	GSC	-32.19	34.46	-99.63 – 35.25	363.50	-0.93	0.35		
	GN*	-78.66	34.39	-145.96 – -11.35	363.50	-2.29	0.02		
	Intercept	185.03	24.32	137.44 – 232.62	363.50	7.61	2.39E-13		

TWS^A shown as reference group to present significant difference relative to other groups. TWS and GN did not differ from each other for any of the other rows in the table.

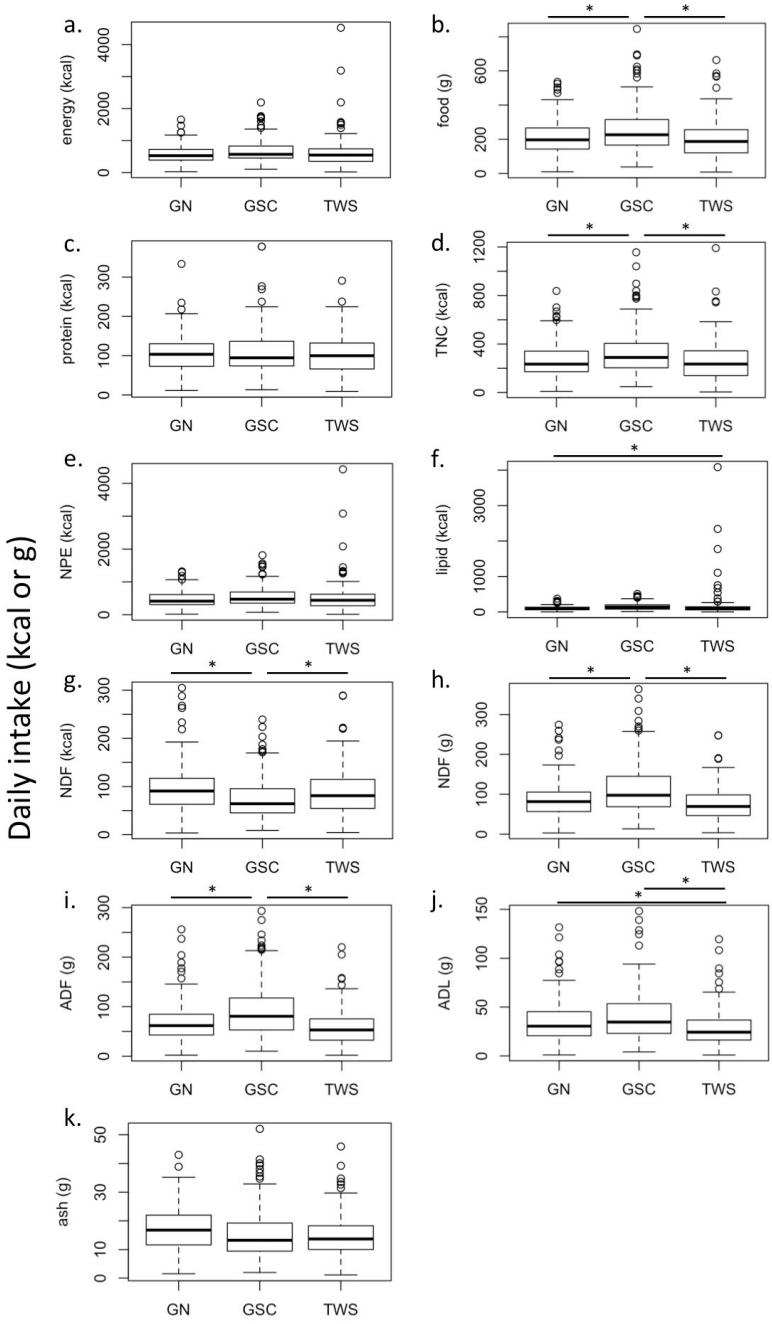


Figure 2.8. Boxplots for daily nutrient intake differences for females in different groups. Boxplots show median and interquartile range. Whiskers represent the most extreme data point, no more than 1.5 * IQR away from the box. Outliers are data points beyond the whiskers. Food (g) included NDF, protein, lipid, TNC and ash. Linear mixed models tested for group differences in daily intake with ID as random effect. See Table 2.6 for model details. *=significance.

Table 2.7. Significant differences in daily intake by females during low versus high fruit availability periods. Linear mixed models had high FAI of fruit as the reference class for the fixed effect, Subject ID nested in Group as random effects and N=371 daily intakes. Only models with a significant effect of fruit availability are presented here. * indicates significance. R^2 values are pseudo- R^2 [Lefcheck, 2016].

Response variable	Predictor	Estimate	SE	95 % CI	DF	T-value	P value	Fixed effects R^2	Random effects R^2
ADF (g)	FAI (high)							0.03	0.15
	low*	19.34	5.77	7.98 – 30.67	350.00	3.35	9.00E-04		
	Intercept*	59.05	11.15	34.85 – 83.25	2.90	5.30	0.01		
NDF (kcal)	FAI (high)							0.02	0.07
	low*	17.40	6.18	5.24 – 29.55	350.40	2.81	0.01		
	Intercept*	74.41	8.27	57.42 – 91.40	4.60	9.00	0.00		
NDF (g)	FAI (high)							0.02	0.12
	low*	21.58	6.78	8.25 – 34.88	350.40	3.19	1.58E-03		
	Intercept*	76.68	12.20	50.39 – 102.96	3.00	6.28	0.01		
ADL (g)	FAI (high)							0.02	0.09
	low*	8.99	2.94	3.21 – 14.76	350.70	3.06	2.39E-03		
	Intercept*	29.18	4.52	19.64 – 38.72	3.60	6.45	4.13E-03		

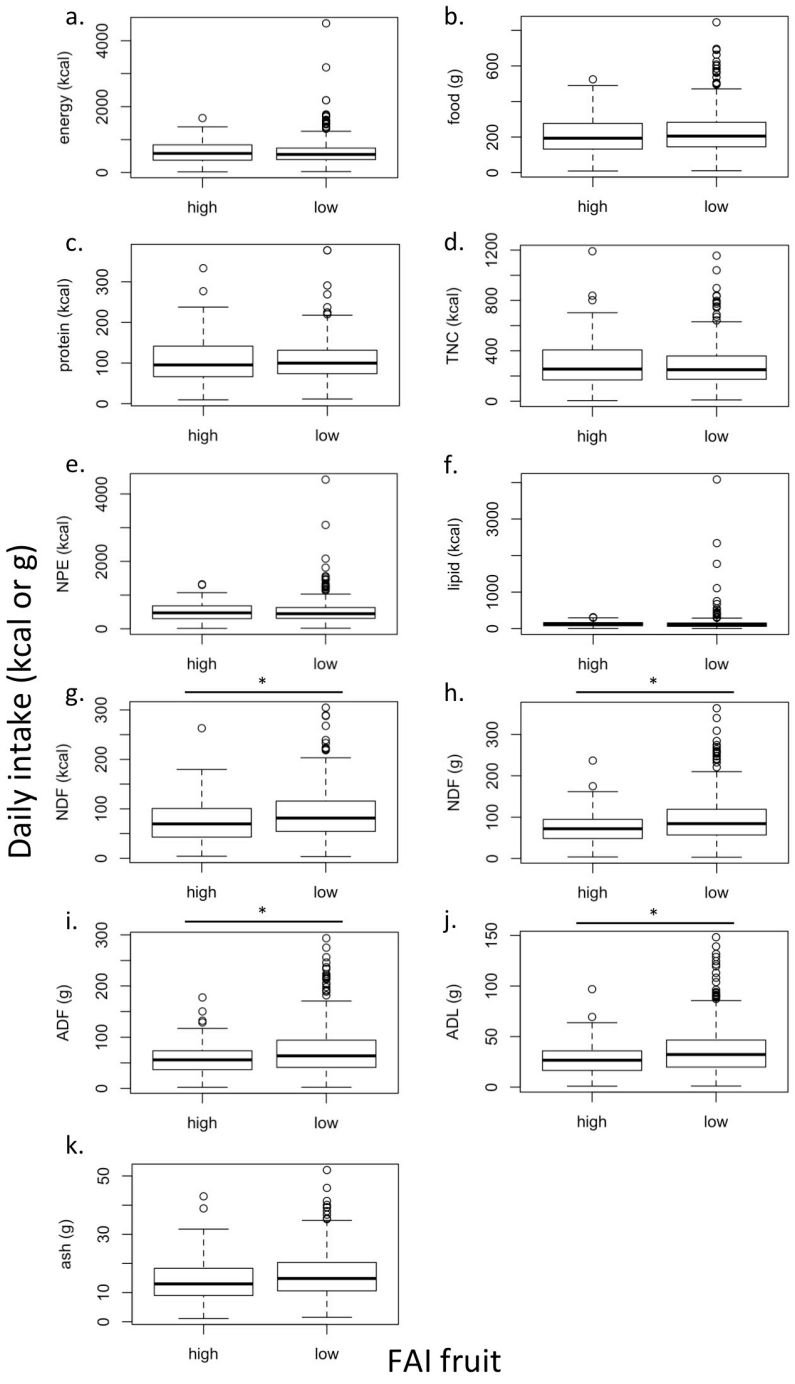


Figure 2.9. Boxplots for daily intake differences of females in periods of low versus high fruit availability. Food (g) included NDF, protein, lipid, TNC and ash. Linear mixed models tested for differences in daily intake with Subject ID nested in Group as random effects. See Table 2.7 for model details. * indicates significance. See Figure 2.8 for boxplot explanation.

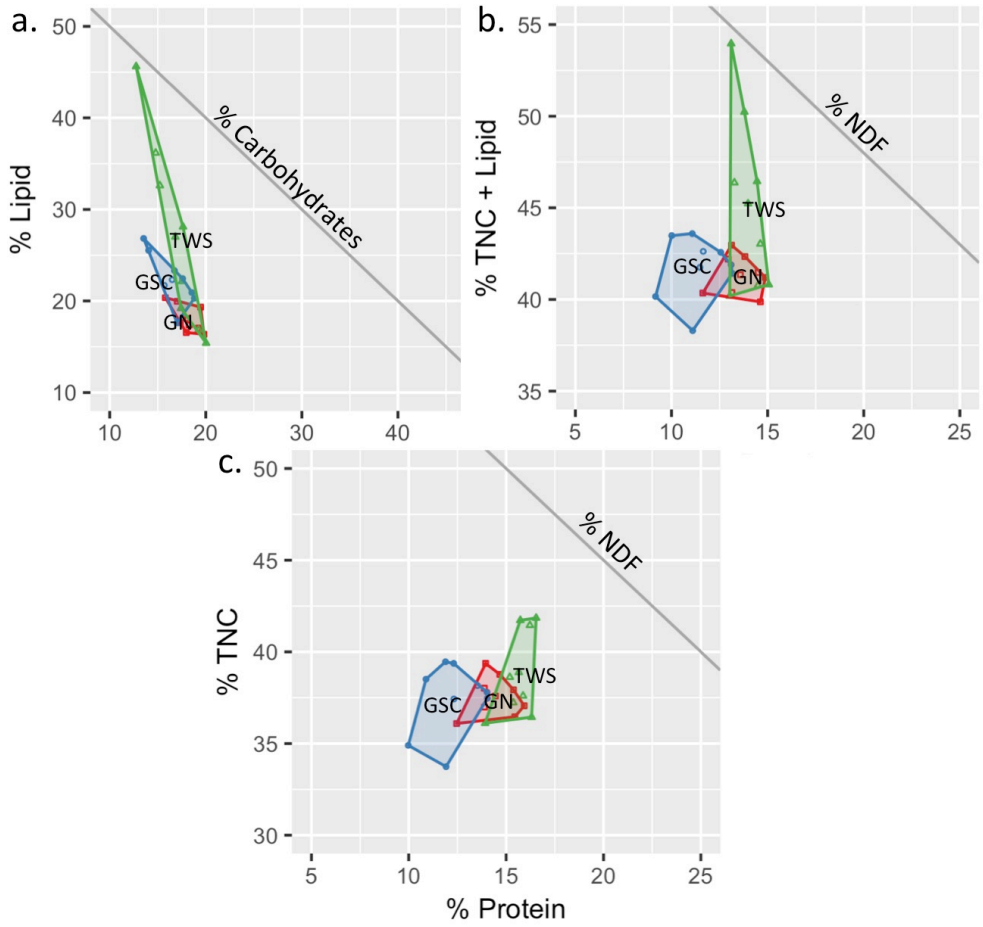


Figure 2.10. RMTs of individual daily diet intake means. The axes (x-, y- and implicit i-axis) are as follows: a) Protein x Lipid x Carbohydrate (relative percentages (by kcal)), b) Protein x TNC+Lipid x NDF (relative percentage (by grams)), c) Protein x TNC x NDF (relative percentage (by grams)). In a) the caloric value of structural fiber (NDF) in diet was calculated using group-specific digestion coefficients, see Methods for more details. A point's position indicates relative proportions of the three axis parameters. Color and symbol type indicate group identity, with colored polygons uniting points from each group (8 subjects per group). Each point represents mean daily intake of a subject over the study period (mean 15.46 female-days per individual, N=371 female-days total). Group labels show position of point representing the group grand mean.

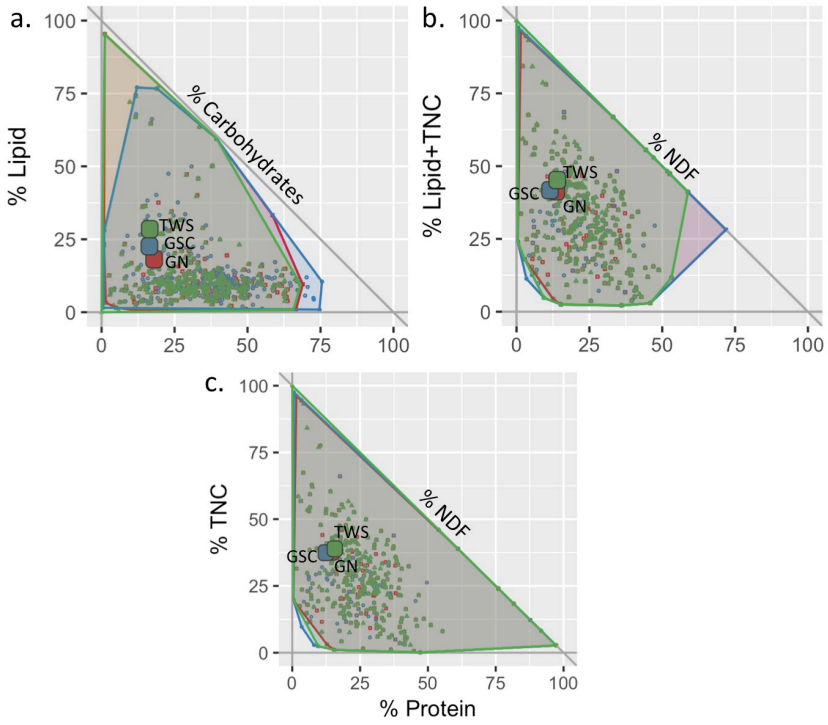


Figure 2.11. RMTs of group diet menu and grand mean group daily diet intakes.

The axes (x-, y- and implicit i-axis) are as follows: a) Protein x Lipid x Carbohydrate (relative percentages (by kcal)), b) Protein x Lipid+TNC x NDF (relative percentage (by grams)), c) Protein x TNC x NDF (relative percentage (by grams)). In a), caloric value of structural fiber (NDF) in diet was calculated using group-specific digestion coefficients, see Methods for details. Polygons represent possible diets while solid rectangles represent observed group diets (grand means (8 subjects per group, mean 15.46 female-days per subject)). Each of the three polygons represent the "nutritional space" of a group's diet menu where a point represents a species-specific food item known to be eaten by females in the group. Color and symbol type indicate group identity. A subject could consume a diet that fell anywhere within the nutritional space bounded by the polygon by consuming a mixture of the different foods composing the polygon. See Appendix V for Figure 2.11a using only important foods (those contributing >1% of calories consumed by group).

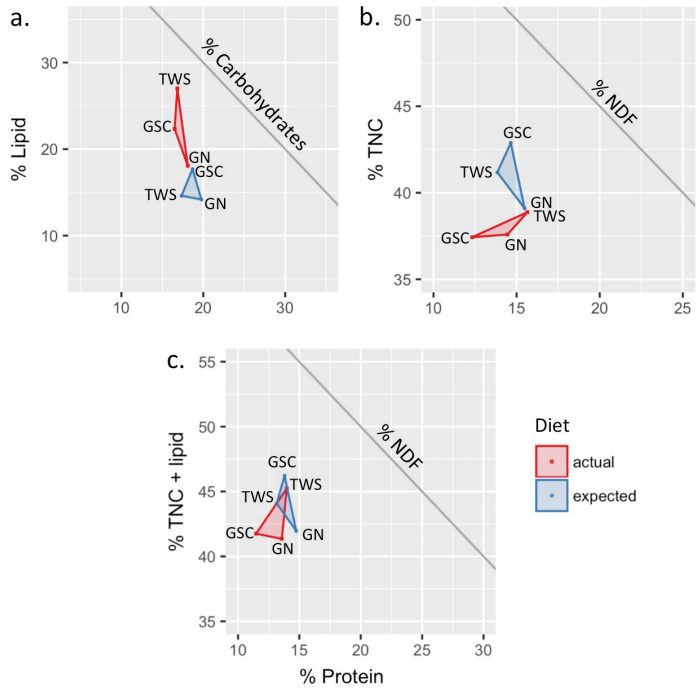


Figure 2.12. RMT comparisons of expected diets (based on relative food availability) and observed daily diet intakes. The axes (x-, y- and implicit i-axis (unlabeled on figure)) are as follows: a) Protein x Lipid x Carbohydrate (relative percentages (by kcal)), b) Protein x TNC x NDF (relative percentage (by grams), c) Protein x TNC+Lipid x NDF (relative percentage (by grams)). In a), caloric value of structural fiber (NDF) in diet was calculated using group-specific digestion coefficients, see Methods for details. Polygon color indicates the groups' expected (blue) or observed (red) diet. I calculated expected diet by first weighting species-specific phenology data for various plant parts (fruit, young leaves, mature leaves, flowers and flower buds) by their relative availability (based on transect data), and second, multiplying by the nutritional value of foods, and finally averaging diets over group (N=16 expected diets per group, spaced every 2 weeks between January-September 2015 [Raubenheimer et al., 2015]). I calculated observed diets using data from daily focal follows and nutritional value of foods as grand mean intakes for a group (N=8 subjects per group,) and for the population (N=24 subjects, mean 15.46 female-days per subject).

Table 2.8. Grand mean daily path length (DPL) for individual females, by group and for the population. Grand means were calculated first by averaging DPLs by individual (N=15-16 per individual), then averaging across individuals within a group (N=8), or within the population (N=24).

	Grand mean DPL (m)	SD	N
GN	758	60	8
GSC	877	90	8
TWS	783	101	8
Population	806	97	24

Table 2.9. Linear mixed model for predicting daily path length (N=371 female-days). As expected, the number of GPS points increased DPL and rainfall decreased DPL. * indicates significance. R^2 values are pseudo- R^2 [Lefcheck, 2016].

Fixed effects	Estimate	SE	95% CI	DF	t-value	p-value
Variables of interest						
Percentage of fruit in diet*	-1.29	0.54	-2.39 – -0.28	360.70	-2.37	0.02
Daily group size	-6.62	2.74	-10.97 – -2.22	1.20	-2.42	0.22
Centered FAI ripe fruit (/100)	0.79	0.55	-0.24 – 1.91	349.00	1.44	0.15
Centered FAI young leaves (/100)	-0.24	0.35	-0.92 – 0.44	348.60	-0.70	0.49
Daily caloric intake	0.03	0.03	-0.04 – 0.09	358.40	0.79	0.43
Intercept	175.18	283.01	-309.84 – 739.31	33.70	0.62	0.54
Control variables						
Number of GPS counts*	48.96	13.13	21.56 – 72.65	357.00	3.73	2.23E-04
Monthly rainfall*	-0.42	0.11	-0.63 – -0.20	347.70	-3.85	1.39E-04

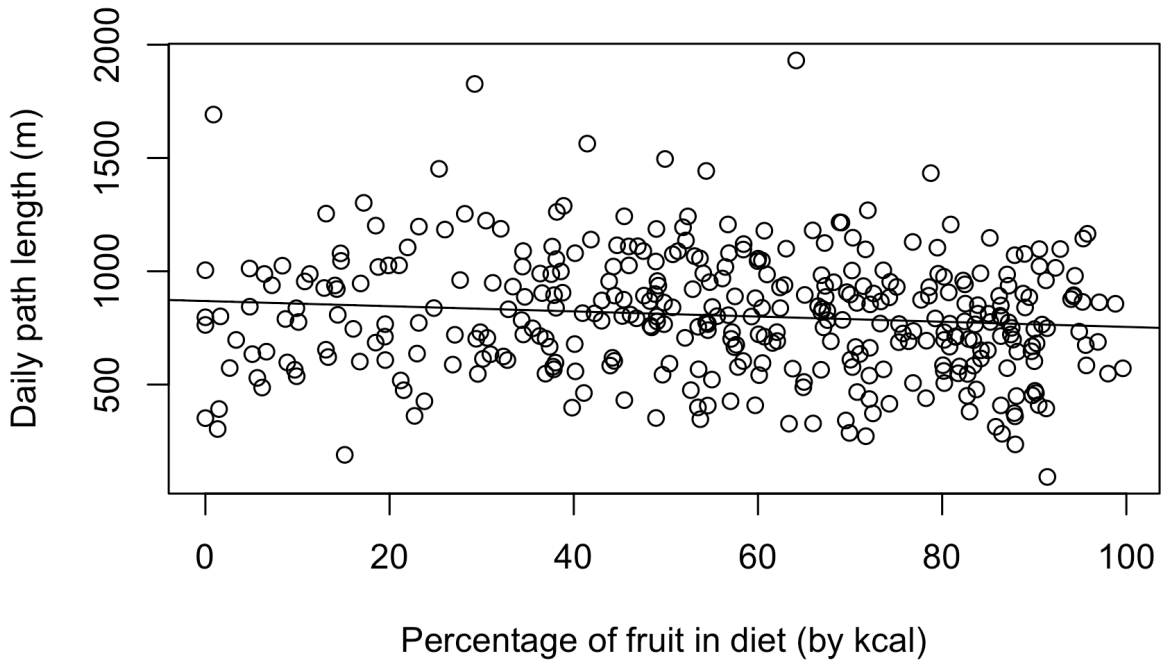


Figure 2.13. Relationship between daily path length and percentage of fruit in diet. The relationship is negative and significant. Each point represents a daily path length (N=371). Black line shows trendline of predicted values of DPL.

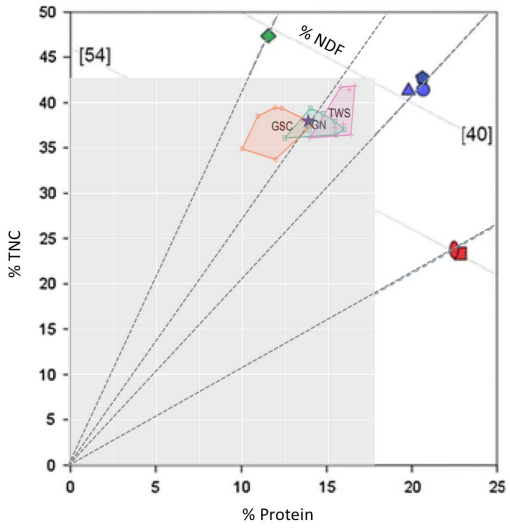


Figure 2.14. RMT of Kakamega blue monkey diet compared to other guenons, chimpanzees and gorillas in other East African locations [Conklin-Brittain et al., 1998a; Raubenheimer et al., 2014; Rothman et al., 2007]. Y-axis was the relative percentage (in grams) of total non-structural carbohydrates (TNC) in the diet. X-axis was the relative percentage (in grams) of available protein in the diet. The implicit I-axis was the relative percentage (in grams) of structural carbohydrates, measured via neutral detergent fiber (NDF) in the diet. Data from this study are shown in the grey-shaded portion, with each point representing a subject's mean daily intake over the study period (N=24 subjects, mean 15.46 female-days per individual). The purple star represents the population mean. White portion of figure is copied from Figure 3 of Raubenheimer et al. [2015], that used data from Conklin-Brittain et al. [1998a] and Rothman et al. [2007]. Green diamonds represent chimpanzees from Kibale National Park, Uganda. Also from that location, the blue circle represents the diet of blue monkeys, blue pentagon represents the diet of red-tailed monkeys, blue triangle represented diet of mangabeys. Red ellipse represents diet of gorillas from Virunga and red square represents diets of gorillas from Bwindi. All diets on white figure were plant-derived diets, from time-based estimations of annual diets. Radials show the TNC:protein ratio.

Table 2.10. Plant species previously found in the diet of Kakamega Forest blue monkeys [Cords, 1987] that were not observed to be consumed during the present study.

Plant species
Acacia monticola
Albizia grandibracteata
Chrysophyllum albidum
Cissus oliveri
Clausena anisata
Clerodendrum silvanum
Combretum molle
Craibia brownii
Deinbollia kilimandscharica
Dicliptera laxata
Fagaropsis angolensis
Illigera pentaphylla
Maerua triphylla
Oncinotis inandensis
Pavonia urens
Pyrrosia schimperara
Rawsonia lucida
Strychnos sp.
Syzygium cumini

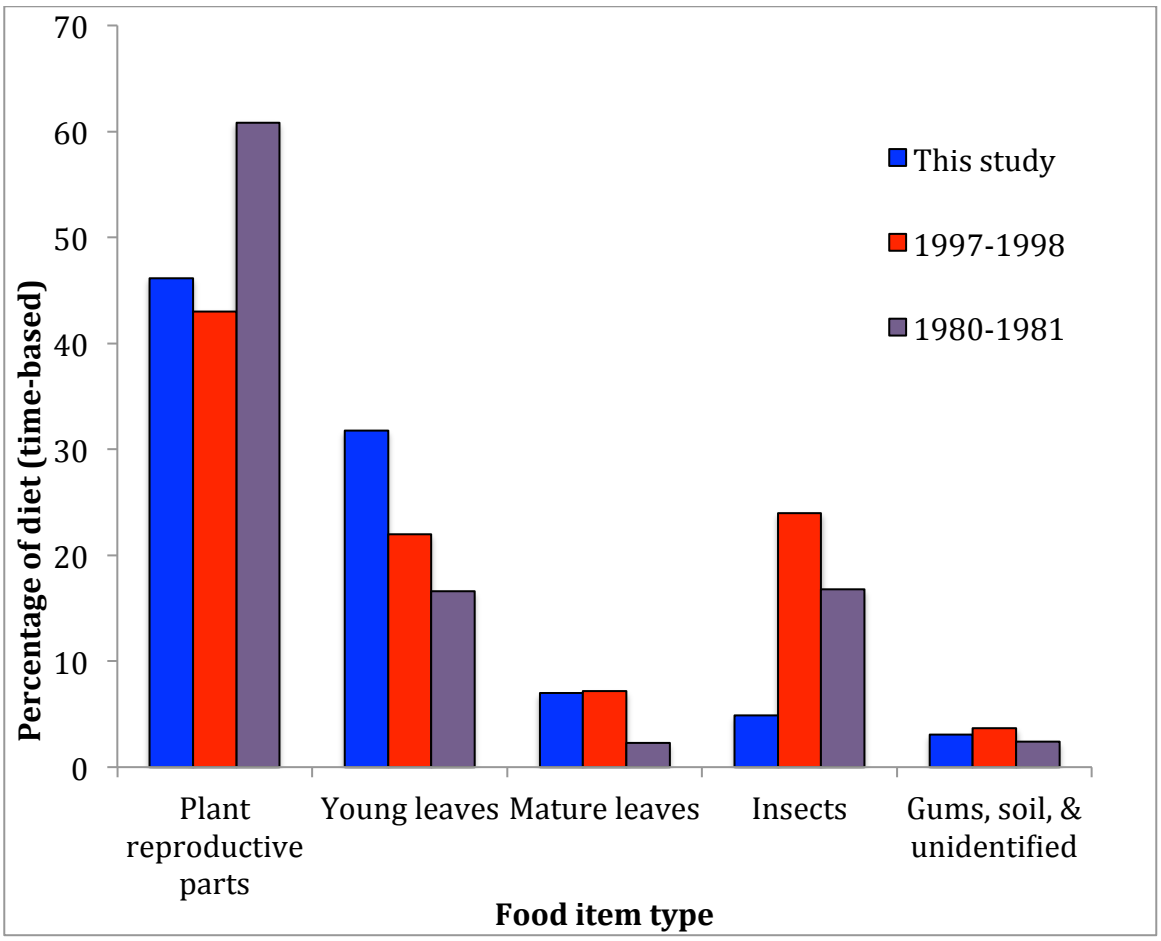


Figure 2.15. Longitudinal comparison of diet compositions of female Kakamega blue monkeys. Percentage of diets based on different observational methods: scan sampling for 1980-1981 diet from Cords [1986]; focal follows for 1997-1998 diet from Pazol and Cords [2005]; time spent feeding based on full-day focal follows for this study. Food item types are ordered by descending order of values from this study.

Table 2.11. Range of percentages of food item types reported in blue monkey diets.

Diet composition data presented from other studies were based on feeding observations, fecal analysis and stomach content analysis (all study periods included at least 6 months of data). For this study, leaves include young leaves, mature leaves and leaf buds and flowers include flowers and flower buds. Percentages for this study represent population means (N=371). Food item types are listed in descending order by maximum percentage.

Food item type	Min %		Max %		This study
Fruit	28	Butynski, 1990	91	Lawes et al., 1990	39
Leaves	2	Lawes et al., 1990	52	Twinomugisha, 2006	44
Animal matter	0	Moreno-Black & Maples, 1977; Lawes et al., 1990	38	Butynski, 1990	5
Flowers	0	Twinomugisha, 2006	20	Schlichte, 1978	7
Fungi	0	Multiple studies	2	Coleman, 2013; Coleman & Hill, 2014	<1

CHAPTER 3: THE NUTRITIONAL STRATEGY OF ADULT FEMALE BLUE MONKEYS: DAILY PROTEIN PRIORITIZATION AND LONG TERM MACRONUTRIENT BALANCING

INTRODUCTION

Dietary generalists make choices among many available foods that determine the amounts of different nutrients that they can use in growth, maintenance, and reproduction. Generalist feeders nonetheless consume a diverse diet, and there is evidence that dietary breadth confers fitness benefits [Pennings et al., 1993; Lefcheck et al., 2013; Senior et al., 2015]. Generalist vertebrates often use strategies that reflect the flexibility of their feeding behavior in response to interspecific feeding competition [Lambert, 2002a], variation in the density of prey [Dell'Arte et al., 2007] and access to nutrient-dense, human-derived foods [Muruthi et al., 1991]. The flexibility and range of feeding behavior in generalist vertebrates may be even more complex than previously known, as a surge of interest in nutritional ecology in the past decade has begun to reveal.

A recent method for studying nutritional ecology is the geometric framework (GF), a state-space model that can assess multiple potentially relevant nutritional (micro or macro) or non-nutritional (anti-feedants, energy) parameters that guide an animal's feeding decisions [Simpson & Raubenheimer, 1995; Felton et al., 2009a; Raubenheimer et al., 2009]. Empirical studies based on this model have shown that achieving a balanced ratio of nutrients underlies the foraging behavior of many species, from slime molds to large vertebrates [Simpson & Raubenheimer, 1995; Raubenheimer & Simpson, 1997; Dussutour et al., 2010; Erlenbach et al., 2014; Felton et al., 2016]. The *nutrient balance* can be visualized as a line through nutrient space, with each axis

representing a critical nutrient. Over a given period (e.g. a day), there is a point on this line, the *nutritional intake target* (hereafter intake target), which is the amount and balance of nutrients needed for optimal performance and adjusted for inefficiencies in the digestive system [Simpson & Raubenheimer, 2012]. When available foods do not provide an optimal balance of nutrients, a consumer will *prioritize* one or more critical nutrients, allowing the ingestion of less critical nutrients to fluctuate around the optimum. These deviations characterize the animal's *rules of compromise*. Overall, an animal will demonstrate a *nutritional strategy*, a balanced intake with or without particular rules of compromise and prioritization of one or more nutrients, to approximate, as closely as possible, its intake target. The animal will also demonstrate a *feeding strategy*, which refers to the feeding behavior and specific food items (species-specific plant parts or animal prey) consumed, to reach a particular intake target. The GF allows one to examine how animals link feeding strategies to nutritional strategies. It may be particularly helpful in studies of dietary generalists, whose flexible feeding behavior might obscure a consistent underlying pattern.

Many primates are considered dietary generalists and flexible feeders, though what those characterizations mean exactly in terms of nutritional requirements (and flexibility of those requirements) is not well defined [Lambert, 2011]. In maintaining a nutritional balance, generalist primates face particularly complex feeding decisions because they can access hundreds of possible food items that vary in nutritional value [Chapman et al., 2003; Rothman et al., 2013]. In addition, the particular foods consumed to achieve a nutritional balance may vary in availability and quality over space and time [Rothman et al., 2007]. Furthermore, the nutritional balance and targets themselves may differ between individuals and vary over individuals' lifetimes, based on physiological demands, and so may differ with age, sex and

reproductive status [Rothman et al., 2008b; Simpson & Raubenheimer, 2012]. However, the parameters (i.e. which and how much of each nutrient) of these balances and targets, and the factors (e.g. seasonal food availability or reproductive food competition) that govern whether primates are able to meet them, are not yet well known.

Studies of primates have begun to show that *nutritional* strategies vary across species, locations, seasons, and age-sex classes [Rothman et al., 2007, 2008b, 2011; Felton et al., 2009b; Johnson et al., 2013]. Several studies suggest that balancing non-protein energy (NPE, i.e. carbohydrates+lipid) to protein (NPE:P) may be critical, though exact ratios varied by species (1.6:1 to 9.5:1; [Felton et al., 2009b; Rothman et al., 2011; Simpson & Raubenheimer, 2012; Johnson et al., 2013, 2017; Irwin et al., 2015; Martínez-Mota et al., 2016]). Maintaining species-specific goals may mean that feeding strategies differ by location, according to what a specific habitat offers. For example, the diets of different mountain gorilla (*Gorilla beringei beringei*) populations differed in plant species and parts consumed, though they contained similar percentages of nutrients overall [Rothman et al., 2007]. Similarly, populations of red colobus monkeys (*Procolobus rufomitratus*) consumed the same concentrations of fiber and protein even though dietary components varied with habitat, which encompassed heavily logged to undisturbed forest [Ryan et al., 2012]. Regardless of location, evidence supports the idea that primates regulate intake across time. A month-long study on a single female chacma baboon (*Papio hamadryas ursinus*), for example, showed that an individual can, at least for a short period, regulate its diet on a daily basis to balance nutrients cumulatively [Johnson et al., 2013]. Over longer periods, though, primates may not have adequate resources to balance intake. For example, over 9 months, spider monkeys (*Ateles chamek*) prioritized protein, allowing non-protein energy intake to fluctuate [Felton et al., 2009b]. Two groups of black howler monkeys

(*Alouatta pigra*) also seemed to prioritize protein across three rainfall periods characterized by dietary shifts (i.e. protein intake did not correlate with shifts in diet), while non-protein energy intake varied and correlated with the amount of ripe fruits consumed [Amato & Garber, 2014]. Seasonal changes in food availability may lead primates to change their nutrient balance. Gorillas balanced protein and non-protein energy, but changed the ratio of these components over seasons based on whether fruit or leaves dominated the diet, according to their availability [Rothman et al., 2011]. In contrast to the black howler monkeys, they prioritized non-protein energy, keeping it at a consistent level across seasons, and consuming excess protein during the leaf-dominated period. Finally, balance or targets may vary by age-sex class. Gorillas, orangutans, chimpanzees, and Verreaux's sifakas show such variation in macronutrients consumed, with differences possibly related to the demands of growth or reproduction [Rothman et al., 2008b, 2011; Pokempner, 2009; Koch et al., 2017; Vogel et al., 2017].

The growing number of nutritional ecology studies from natural populations indicates that primate feeding is complex, species-specific, and that more research is needed to pinpoint the factors that influence both the nature and diversity of nutritional strategies in natural populations. To contribute to this challenge, I explored the nutritional ecology of a generalist primate, the blue monkey, *Cercopithecus mitis*. Blue monkeys have a wide geographic range in African forests, occurring in various forest types [Lawes et al., 2013]. Their ability to be both largely folivorous and frugivorous seems to enable them to persist in disturbed forests [Struhsaker, 1978; Thomas, 1991; Lawes et al., 2013]. With annual diets including >125 plant species in a single population, they presumably regularly make decisions about which foods to consume. Though they prefer ripe fruit, they switch frequently from one food to another, like other guenons [Lambert, 2002a], and consume leaves on a regular basis [Lawes et al., 2013].

Their most important food classes – fruits, leaves, and insects – constitute highly variable portions of their feeding time in different populations and periods (e.g., fruits 28-91%, leaves 15-52%, insects 5-45% [Cords, 1987; Butynski, 1990; Lawes et al., 1990, 2013]). Blue monkeys can ferment foods in the ceaco-colon region, demonstrating morphological adaptations that facilitate dietary flexibility, and especially enhanced folivory, relative to closely related taxa [Bruorton & Perrin, 1988, 1991; Lambert, 2015]. Relatively slow gut passage rates also aid in digestion and absorption [Lambert, 1998, 2002b; Blaine & Lambert, 2012], and likely permit dietary breadth. Overall, then, these monkeys are able to exercise considerable flexibility while feeding.

Blue monkeys are also group-living, which may influence an individual's food choices. Feeding competition (contest or scramble) with group-mates may lead individuals to increase dietary breadth [Lambert, 2011] or alter their nutritional strategy. Blue monkeys are thus an ideal taxon in which to study how nutritional strategies of generalist primates are shaped by the physical and social environment. My study, which focused on adult females, also evaluated the effects of reproductive demands. Combining behavioral observations in the field with laboratory analysis of the nutritional content of a large set of food samples, I addressed the following hypotheses:

(H1) Like other animals, blue monkeys choose foods to balance critical nutrients on a daily basis. If so, I expected individuals to converge on a daily nutrient consumption ratio. I also examined evidence that individuals employed rules of compromise when available food did not allow the diet to approximate the target intake. I predicted that blue monkeys would prioritize protein intake, like another frugivorous primate (spider monkeys, [Felton et al., 2009a; b]) and a generalist primate (humans, [Simpson & Raubenheimer, 2005, 2012]).

(H2) On a daily basis, time spent in different habitat types, fruit availability, and/or the amount of fruit in the daily diet affects daily nutrient balance or intake of critical nutrients of subjects. Here, I examined the relationship between habitat use and diet on a more fine-grained scale than in Chapter 2. Results presented there demonstrated that females, over the course of the study period, and despite being in groups with differential access to multiple habitat types, converged on overall diet compositions that were similar in plant parts. However, in doing so, females in different groups used different species of plants and had varying dietary breadth. Dietary breadth is based on availability of preferred foods and blue monkeys will often adjust ranging patterns accordingly: across populations, when fruit is abundant, groups range widely to access favored fruit, but they consume a more diverse diet and range less far when fruit abundance is lower. At the lowest fruit abundance, groups range the most widely, apparently seeking out high quality food [Omar & de Vos, 1970; Rudran, 1978a, b; Schlichte, 1978; Scorer, 1980; von dem Bussche & Van der Zee, 1985; Beeson, 1987, 1989; Cords, 1987; Butynski, 1990; Lawes et al., 1990, 2013]. Thus, depending on fruit availability, one might expect blue monkeys to use different habitat types to access habitat-specific food resources.

(H3) Social dominance may influence nutritional strategies, allowing higher-ranked subjects to meet nutritional goals more effectively. To date, the effect of dominance rank on nutritional strategies (including balances, prioritizations and compromise) has not been reported in any animal. However, given that high rank enables priority of access to resources, it is likely that higher ranked females could balance nutrients more tightly, whereas lower ranked females may show more fluctuation either on a daily or on a seasonal basis. Female blue monkeys show clear, stable dominance hierarches [Klass & Cords, 2015], though fitness advantages of high rank seem weak [Lawes et al., 2013; Roberts & Cords, 2013]. However, prior research suggests

that rank may be important when females feed on preferred foods [Foerster et al., 2011]. Aggression occurs disproportionately during feeding, and especially when monkeys feed on fruits [Cords, 2000; Pazol & Cords, 2005; Foerster et al., 2011]. Additionally, lower-ranked females spent less time than higher-ranked females feeding on fruits when these were rare [Foerster et al., 2011]. Thus one might expect lower-ranked females to employ more costly nutritional strategies, consuming lower-quality foods that provide nutrients in a less balanced ratio.

(H4) Nutritional strategies of females are influenced by their reproductive demand: specifically, pregnant/lactating females shift their nutritional balance relative to non-reproductive females. It is likely that reproductive females aim for a lower NPE:P ratio (more protein in diet) given that protein is important for fetal development, or alternatively these females consume more energy overall than non-reproductive females. On one hand, studies on captive primates suggest that adults require 5-8% of their energy as protein, whereas a pregnant or lactating female may require 12.5% of her energy as protein [Oftedal, 1991]. On the other hand, Kakamega blue monkeys appear to be energetically challenged during their reproductive cycle, with higher values of glucocorticoid hormones in the second half of pregnancy and the first six months of lactation [Foerster et al., 2012]. Moreover, there may be an interaction between reproductive demand and dominance rank, as only among lactating blue monkeys and regardless of fruit availability were glucocorticoid hormones higher for lower ranking individuals [Foerster et al., 2011].

METHODS

Data collection

Methods for nutritional ecology studies of primates comprise two main parts: 1) field work to sample behavior, monkey feces and food, and 2) laboratory analysis of physical samples for nutrient composition. I used standard methods outlined by Rothman et al. [2012, 2013]. To characterize Kakamega vegetation, I followed methods of Foerster et al. [2012].

Study site: The Kakamega Forest, western Kenya (ca. 238 km^2, 1650 m elevation) is a patch of semi-deciduous Guineo-Congolian rainforest [Kokwaro, 1988; Mitchell, 2004]. This study occurred at a ca. 2 km^2 long-term research site (0^o 19' N, 34^o 52' E [Cords, 2012]. Rainfall averaged 222 mm per month during the study period (January-September 2015) with fluctuations generally matching longterm norms (Figure 2.2, [Chap 2]). As a result of human activity (both governmental forest management and activities of local people) and variable soil conditions, the forest is a mosaic of habitat types on a small scale [Mitchell, 2004; Mitchell et al., 2009].

For the purposes of this study and with reference to the vegetation classes described by BIOTA as part of their extensive ecological research [Mitchell, 2004; Mitchell et al., 2009], I identified three habitat types: near-natural forest, forest village, and human-modified forest [Chap. 2]. Habitat types differed in mean plant basal area, species composition of main trees, and species prominence of main trees (Table 2.1, [Chap 2]). Near-natural forest comprised mainly mature secondary growth of native trees, interspersed with a few individuals of non-native species such as *Bischofia javanica*. Compared to the other two types, near-natural forest had relatively dense understory vegetation. Mean basal area of plants with DBH (diameter at breast height) ≥ 5 cm was similar in the near-natural forest and farm/plantation forest (59.3 and 60.6 m^2 per ha respectively). Farm/plantation forest included monocultures of exotic species (*B. javanica, Grevillea robusta)* and abandoned farmland with large, dispersed *Eucalyptus saligna* and occasional *B. javanica,* overgrown by guavas (*Psidium guajava)*. Vegetation was more

homogeneous than in the other two habitat types (i.e. the top five species of plants comprised 88% of mean basal area per ha in farm/plantation forest, versus 51% in near-natural forest and 50% village forest; Table 2.1, [Chap 2]). While farm/plantation forest occurred mainly in the southern part of the study site, there was a small patch close to the forest village, predominately *Pinus patula*, upon which blue monkeys did not feed. The forest village (7.9 ha) included scattered Kenya Forest Service buildings and roads, and a tree nursery. Land cover included grass and heterogeneous tree cover that was sparse compared to the adjacent near-natural forest, but dense enough that monkeys could travel through the village via arboreal pathways, and large enough to allow animals to congregate for social activity like grooming.

Subjects: This population of blue monkeys has been under study since 1979, with the number of individuals monitored at one time growing over the years as groups slowly grew and fissioned [Cords, 2012]. Group density has changed little, as study groups expanded the area that they used ([Cords, 2012], unpub. data). Population density has also remained quite stable (1979-1981 estimate: 198 ind/km^2, 1994-1998 estimate: 220 ind/km^2; 2006-2010 estimate: 192 ind/km^2 [Fashing & Cords, 2000; Fashing et al., 2012]. The growth of the study groups and stability of the population suggests that monkeys had access to adequate food and nutrition over the long term. Additionally, daily path length, a proxy for energy expenditure, did not significantly correlate with daily energy intake [Chap 2], suggesting that subjects were not energetically constrained.

Subjects were 24 adult (parous) females, 8 from each of three study groups (TWS, GSC, GN), of differing ranks and reproductive states (births occur seasonally, every 2-3 years per individual; [Cords & Chowdhury, 2010]). The groups' home ranges varied in size (by a factor of 2) and habitat composition (with near-natural forest accounting for 56-92% of each home range

(Table 3.1, Table 2.2 and Figure 2.3 [Chap 2]). Subjects used all habitat types for feeding, resting, and socializing.

Dominance rank: I used information on dominance rank from Cords' long-term project [Klass & Cords, 2015]. Dominance ranks, based on matrices of decided (clear loser) dyadic agonistic encounters (from October 2014-October 2015), were derived using the I&SI method as implemented in DomiCalc [Schmid & de Vries, 2013]. I expressed females' ranks on a 0-1 (lowest-highest) scale in each group.

Reproductive demand: I assigned a female's reproductive demand for each date using information on her infant's age from estimated conception date. Near daily observations of all study groups, even prior to this study, generally allowed assignment of an infant's birthdate to ± 1 day. I used birthdates to back-date the conception date, assuming a gestation length of 176 days [Pazol & Cords, 2005]. I coded reproductive demand in six categories: early gestation (first half), late gestation (second half), early lactation (up to 6 months after birth, by which time infants spend <5% of time on the nipple; [Foerster & Cords, 2002]), mid-lactation (7-12 months), and late lactation (13-24 months, or until the mother conceived again, see below). The post-natal age cut-offs reflected information on how quickly daily records of suckling decline with age (steeply for the first 6 months, moderately during the second 6 months, more gradually during the second year; Cords, unpub.). Females with no infants <2 years (and also not pregnant) were considered non-reproductive. Some females had infants at 1-2 year intervals, and therefore were both suckling one infant (>1 yr old) while pregnant with the next one. Because infants >1 year old (late lactation stage for mother) suckle infrequently (at least during the day), I assumed that the demands of late lactation were minimal compared to those of gestation, and prioritized gestation in classifying the females' reproductive demand. This assumption seemed reasonable since mean

intakes of protein and energy were similar for females in the categories of early gestation (653 kcal/day, 106 kcal of protein, N=22 female-days), late lactation (637 kcal/day, 112 kcal of protein/day, N=96 female-days) and late lactation + early gestation (676 kcal/day, 102 kcal protein/day, N=21 female-days).

Behavioral observations: A team of observers conducted all-day focal follows [Altmann, 1974] on each subject approximately twice a month for 8 months, spacing repeated samples of each individual at >1 week intervals (mean 15.4 days ± 5.9 SD). All-day focal follows are recommended for studies of nutritional ecology [Felton et al., 2009a; Rothman et al., 2012, 2013]. During follows, subjects occasionally went out of sight, but average "in-sight" time was 9.1 ± 0.2 hr (out of sight time averaged 0.7 ± 0.2 hr; [Chap 2]).

Using tablets running Microsoft Office 365's Excel application, team members recorded the duration of each focal animal's feeding bouts, as well as the species and part of all plant food items and morphotype of insects for each feeding bout [Chap 2]. Feeding bouts started when food first touched a subject's mouth and continued as long as she was taking bites and/or chewing. Team members did not stop bouts if she continued to hold the food between these acts of ingestion (there were often brief pauses of a few seconds); however, if a female paused for vigilance or other alarm responses, team members stopped the bout. Team members noted how individuals processed food (e.g. spit seeds or peeled stems before consumption) and recorded quantities eaten using standard units that were easy to differentiate (e.g. one *P. guajava* fruit, a 1-inch section of *B. javanica* stem). With a continually updated list of blue monkey plant foods, observers were able to identify most plants in the field; in the few cases where the food was unknown, the team consulted local forest guides for plant identification.

Habitat use: To track each subject's use of habitat types throughout the day, observers recorded GPS coordinates at 30 min intervals, on the hour and half hour, using a handheld GPS unit (Garmin GPSMAP® 60 CSx) with errors less than ±5 m. We missed some scheduled GPS records when the focal subject's exact location was unknown [Chap 2].

Food sample collection: Whenever possible, I collected samples of plant foods from the same plants that monkeys used for feeding. I collected insect samples from vegetation, and euthanized them via decapitation or ethanol exposure [Ozanne & Bell, 2003]. Insect collection was opportunistic [Rothman et al., 2013], as insect feeding was quick and generally precluded simultaneous collection. Social insects (like ants) could sometimes be collected at the time of observed feeding. I calculated mean unit weights of fresh food samples, in the same observably consistent amount recorded during focal follows [Rothman et al., 2012, 2013; Chap 2].

I dried plant and insect samples in a custom-built solar-powered dehydrator set to 55° C [Rothman et al., 2012; Chap 2]. Sample drying occurred primarily during the day, and samples typically dried fully over the course of few days, and up to one week. I shielded samples from sun exposure and discarded moldy samples (mold was rare). During the dry season (January-early March), I dried some mature leaf samples in a warm, dark shed that blocked all sunlight, as this allowed additional drying capacity [Rothman et al., 2012].

Fecal sample collection: I collected a fresh fecal sample (approximately 5-10 ml, from the ground or off vegetation) from a given female one day after her focal follow using sterile Corning 15 ml plastic tubes. I sterilized samples and then dried them at 55 ° C [Rothman et al., 2012; Chap 2]. Samples were then sealed in the tube with Parafilm, for future analysis to assess baseline fiber digestibility (see *Nutritional analyses* below; [Rothman et al., 2012; Chap 2]). If it was not possible to obtain a sample from the previous day's focal subject, I tried to collect a

sample from another adult female in the same group, which allowed me to assess a mean value for fiber digestibility.

Food availability: To assess the availability of plant foods, I combined a vegetation survey with phenology monitoring [Marshall & Wich, 2013], using information from the long-term dataset collected by Cords and her team. I combined data from transects measured in 2014 with new transects that were measured as part of my study. Coverage included 36 near-natural forest transects and 10 human-modified forest transects (each transect 100x10m^2). Assistants measured all trees and herbaceous plants with DBH≥5 cm [Ganzhorn et al., 2011; Chap 2]. For the village habitat, where tree coverage was very heterogeneous (plants either clumped or planted in rows along roads), random transects did not appear to assess basal area of plants very accurately. Therefore I measured all trees and herbaceous plants with DBH≥5 cm in the village area used by the study groups (TWS, GN, 6.6 ha total) and scaled the values to make them comparable to transect data on a per hectare basis.

Every 2 weeks, a particular assistant scored ripe fruit and young leaf phenology for 10 stems (typically) of each of 36 main food plant species (those constituting >0.5% of feeding time in ≥3 of 23 group-years (2007-2011) in which adult female feeding behavior was documented by focal animal samples, as well as some unique trees that were heavily used (Cords, unpub.)). One species, an exotic oil palm (*Elaeis* sp.), existed only as a single tree in the village, so I was limited to one monthly score for this species. To quantify ripe fruit availability, the assistant first assessed overall fruit capacity using a semi-quantitative 0-4 scale (0=none, 1=1-25% of maximum capacity, 2=26-50% of maximum capacity, etc.; [Chap 2]) and second, assessed the proportion of fruit that was ripe (0% ripe, 25%, 50%, 100%). I then multiplied fruit capacity

score by proportion ripe to assess ripe fruit availability (e.g. 50 % fruit capacity x 25 % ripe=13 % ripe fruit availability).

I then calculated a plant-part specific (young leaf or ripe fruit) food availability index (FAI) for every bi-weekly phenology scoring and for each group [Chap 2]. For each FAI score, I averaged the basal area of each tree species from vegetation surveys in a particular habitat type, then multiplied this measure by the mean phenology score of that species, and added these products together across all phenology species. I then computed composite scores for each group by weighting the habitat-specific phenology indices according to their representation in the group's home range.

Wet chemistry analyses: I conducted lab work in the Rothman Nutrition Lab, Hunter College, City University of New York. I measured the percentage composition (per gram dry mass) of the following nutritional parameters in monkey foods: structural carbohydrates (cellulose, hemi- cellulose, lignin, measured via neutral and acid detergent fiber (NDF and ADF) and acid detergent lignin analyses (ADL)), available protein (thereafter referred to as protein, subtracting acid detergent insoluble protein from crude protein amount from combustion), ash (i.e. minerals, measured through combustion and correcting for fiber bound ash), and crude lipid (via ether extraction; [AOAC, 1990; Licitra et al., 1996; National Research Council, 2003; Palmquist & Jenkins, 2003; Conklin-Brittain et al., 2006; Rothman et al., 2008a, 2012, 2013]). I computed percentage of TNC by subtracting from one the sum of NDF (i.e. structural carbohydrate estimate), protein, lipid, and ash ([Rothman et al., 2012]; Appendix I).

An animal's gut physiology determines its ability to digest fiber via microbial fermentation. Captive blue monkey females had a mean gut retention time of plastic markers of 20.6 hr ±12.8 SD hours [Lambert, 2002b], so I related an observed daily diet to the fecal sample

collected the following day. To determine energetic gain from fiber, I compared the lignin content in the daily diet to the corresponding fecal sample to calculate the fraction of the ingested fiber that was fermented [Fahey & Jung, 1983; Van Soest, 1994; Rothman et al., 2012]. I calculated fiber digestibility coefficients using published protocols [Conklin-Brittain et al., 2006; Rothman et al., 2008b; Chap 2].

Near infrared reflectance spectroscopy (NIRS) analysis: In addition to wet chemistry, I used NIRS to analyze plant food nutritional composition ([Rothman et al., 2012; Chap 2]; Appendix I). Energy spectra signatures of food samples (from irradiation by near-infrared light) are matched and calibrated against reference values determined via traditional wet chemistry analysis of samples. Calibrated spectra are grouped according to plant parts to create predictive equations, which allow estimation of the nutritional values for samples of the same plant part. This technique had been shown to measure accurately the nutritional content of primate diets [Rothman et al., 2009, 2012].

Additional nutritional values: Blue monkeys consumed eight human foods: chicken egg, maize, *ugali* (cooked maize flour), cabbage, watermelon, sweet potato, orange, and sugarcane (Appendix I). I analyzed maize and *ugali* samples in the lab, and, for the other six foods, used nutritional parameters from the USDA (https://ndb.nal.usda.gov/ndb/). Nutritional values of insect samples were determined using wet chemistry lab techniques by P. Wakaba at the Kenya Agricultural & Livestock Research Organization, Muguga campus.

Daily diet intakes: I calculated daily nutritional intake (in grams) per focal follow by multiplying the observed quantity of food consumed (number of units x unit weight) by the food's nutritional value, then summing these values across all foods consumed. I then converted macronutrient intakes (in grams) to energetic values (kcal) using the following conversions: 4

kcal/g for non-structural carbohydrate, 4 kcal/gram for protein, 9 kcal/g for lipid and 3 kcal/g for fiber [Conklin-Brittain et al., 2006]. The caloric value of fiber was adjusted by multiplication with a fiber digestibility coefficient specific to each group [Conklin-Brittain et al., 2006; Chap 2].

Data analysis

I ran all statistical models and graphics in R, version 3.3.2 [R Core Team, 2016]. I used the following statistical packages in CRAN: MASS [Venables & Ripley, 2002], lme4 [Bates et al., 2015], lmerTest [Kuznetsov et al., 2016], ggplot2 [Wickham, 2009], and piecewiseSEM [Lefcheck, 2016]. I validated all models by checking the residual distribution, plotting residuals against predictors and plotting a Q-Q plot [Zuur et al., 2009; Ieno & Zuur, 2015]. For any model with multiple predictors, I verified that predictors were not collinear by examining Pearson correlation coefficients using a cut-off of 0.8 [Zuur et al., 2009; Ieno & Zuur, 2015].

Nutrient balance and regulation: I first examined the variation in the daily intake of energy and nutrients, calculating descriptive statistics for four macronutrients (protein (kcal), lipid (kcal), TNC (kcal), NDF (kcal)), NPE (kcal) and total energy (kcal), NPE:P ratio, total food intake (g), and NDF (g). From individual means I calculated a grand mean, SD and CV.

To examine nutrient balancing of NPE and P, I ran a linear mixed model with restricted maximum likelihood (REML, [Bates et al., 2015; Kuznetsov et al., 2016]) using NPE as the dependent variable, P as the independent variable and Subject ID nested in Group as random effects. Using a likelihood ratio test with maximum likelihood (LRT; all LRTs mentioned henceforth also used maximum likelihood), I compared the model to a null model (only random effects). The slope of the model indicated the balance, while the P-value evaluated if the two

measures correlated (i.e. if they balanced against one another) and the pseudo-R^2 value evaluated how tightly the ratio was maintained [Lefcheck, 2016].

To examine whether subjects balanced NPE:P in a cumulative way over the course of the study period [Johnson et al., 2013], I ran an OLS regression for each subject, with *cumulative* NPE (recalculated for each observation day) as the dependent variable and *cumulative* protein intake as the independent variable. The aim of this analysis was to assess how *tightly* subjects maintained a cumulative balance between NPE and P, indicated by R^2 values in these regressions [Johnson et al., 2013]. To test whether a female's ability to tightly balance cumulative NPE:P was influenced by her rank, I used a linear mixed model with REML and Gaussian distribution [Bates et al., 2015; Kuznetsov et al., 2016] to model R^2 values as a function of standardized rank, with group as a random effect. As above, I compared the model to a null model using a LRT.

Rules of compromise: To see whether blue monkeys prioritized protein intake, I evaluated whether NPE intake varied as a function of the percentage of protein in the diet. The protein leverage effect means that absolute protein intake (kcal) is prioritized and strongly regulated, and even slight dietary deviations from the targeted protein intake are accompanied by large fluctuations in the amount of NPE consumed, resulting in an imbalance of energy consumption [Simpson & Raubenheimer, 2005]. For example, when an animal consumes a diet with a lower protein percentage than the target amount, the animal will compromise by consuming excess NPE energy (Figure 3.1), resulting in overall energy excess. When an animal consumes a diet with more protein than the target amount, the animal will under-consume NPE (Figure 3.1), resulting in overall energy deficit.

I calculated the daily NPE values that were expected if protein intake was tightly regulated using the formula $(P_t/P_o)-P_t$, where P_t represented the target intake of protein in diet

(assumed to be approximated by the observed mean protein proportion in the diet) and P_o was the proportion of protein in diet [Simpson & Raubenheimer, 2005; Felton et al., 2009b]. I then compared these expected values with the observed values of NPE, and how both changed in relation to the proportion of protein in the diet.

Factors influencing nutritional strategy: To evaluate which factors predicted nutritional strategy, I used linear mixed models with REML and Gaussian distribution [Bates et al., 2015; Kuznetsov et al., 2016] to model daily intake of protein (kcal) and daily NPE:P ratio. I log transformed protein (kcal) to normalize the distribution [Zuur et al., 2010; Ieno & Zuur, 2015]. I did not transform NPE:P ratio because the distribution was approximately normally distributed. For both protein and NPE:P intake, I used the same initial set of predictor variables which included reproductive demand class, rank, proportion of daily time spent in near-natural forest, FAI of ripe fruit, FAI of young leaves, and percentage of fruit in daily diet and an interaction term between reproductive demand class and rank. I included Subject ID nested in Group as random effects. I standardized all continuous fixed effects to aid in comparing their effects, and because they were measured on very different scales (Table 3.2; [Schielzeth, 2010]). I used LRTs to compare a model with vs. without the interaction effect, and after removing non-significant interactions, to compare the resultant full model to a null model (only random effects). I examined 95% confidence intervals of predictor coefficients, as well as Wald p-values, to assess their significance. To assess the overall significance of the one categorical fixed effect (reproductive demand class), I also used a LRT to compare nested models with and without this variable included. I report the summary from the full model since it reflected all fixed effects [Forstmeier & Schielzeth, 2011].

To further evaluate whether rank affected a female's ability to adhere closely to a nutritional strategy, I used additional linear mixed models with REML and Gaussian distributions [Bates et al., 2015; Kuznetsov et al., 2016]. Response variables were daily deviation from population mean NPE:P ratio and daily deviation from mean protein intake (kcal), each expressed either as an absolute value (to capture overall adherence to population mean values) and as a raw deviation (to see whether rank affected the direction of deviation). In addition, I tested whether rank predicted the daily number of unique food items to see if higher ranked females had a narrower daily dietary breadth (either because they fed more efficiently or they had priority of access to preferred foods). I used the same set of predictors for all models: standardized rank (0-1 scale) as a fixed effect and Subject ID nested in Group as random effects. As above, I compared each model to a null model using LRTs.

RESULTS

Intake regulation: On average, daily protein intake varied least (mean=107.9 kcal ± 53.1 SD, CV 49%, N=371) and daily lipid intake varied most (mean=148.1 kcal ± 272.0 SD, CV=184%, N=371, Table 3.3, Figure 3.2 and Figure 3.3). Grand means (averaged first over subject, then across subjects) showed the same pattern. Median nutrient intake did not differ by group, except for lipid intake: seven of eight females in GSC group showed the highest median lipid intakes (Figure 3.3).

Nutrient balance: Female blue monkeys balanced NPE:P in a 3.8:1 ratio (Figure 3.4). Daily protein intake related positively to NPE intake (β=3.79 ± 0.32 SE, 95% CI=3.16 to 4.42, t=11.81, df=369.30, p<2e-16), and explained 27% of NPE variance. The two random factors (Subject ID nested in Group) explained an additional 0.2%. A LRT confirmed the significance of

protein as a predictor of NPE (LRT, X^2(df=1)=119.1, p<2.2e-16). When I excluded outliers (N=6 female-days with NPE:P ratio >3SD from the mean), protein explained 53% of variance in NPE, while random factors explained an additional 2%.

The daily NPE:P ratio varied widely from 1.2:1 to 44.4:1, with a mean of 5.2 and a CV of 68% (N=371 female-days, Table 3.3). Females showed less variation in the NPE:P ratio when the protein intake was greater or equal to the mean (≥ 107.9 kcal protein, N=166 female-days) with CV of 42%, than when the daily protein intake was below average (CV=101%, N=205 female-days). In short, females regulated NPE:P ratio more tightly when protein intake was at or above average.

As expected, every subject in the population balanced cumulative NPE (kcal) and cumulative protein (kcal) over the course of the study period (i.e. there was a significant, positive relationship for each female with p-values<<0.05; Table 3.4, Figure 3.5). All females also *tightly* balanced cumulative NPE:P, with mean R^2=0.98 ± 0.03 SD (range=0.87 to 1.00, N=24 individuals). Females in different groups similarly balanced cumulative NPE:P ratios (mean slope=4.94 ± 0.77 SD, range=4.03 to 6.71, N=24 individuals; Figures 3.5-3.6). A female's rank did not predict how tightly she balanced cumulative NPE:P, represented by R^2 values from a regression of NPE on P (β=4.88E-03 ± SE 0.02, 95% CI=-0.03 to 0.03, df=20.03, t-value=0.32, p-value=0.75; LRT: X^2(df=1)=0.10, p=0.75).

Protein prioritization: Subjects adhered to the graphical expectations of the protein leverage hypothesis (Figure 3.7), indicating that their rule of compromise was to prioritize protein. Blue monkeys most tightly regulated protein, consuming a mean daily target intake of 107.9 kcal ± 53.1 SD (N=371), which resulted in NPE intake responding to protein content in the diet (i.e. protein leverage). Thus blue monkeys regulated protein intake and subjects consumed a

wide range of NPE, from 11.2 to 4426.9 kcal/day (mean 529.1 ± 384.3 SD, N=371, Figure 3.8). As the percentage of protein in the daily diet increased, consumption of NPE decreased hyperbolically, according to the predictions of the protein leverage hypothesis [Simpson et al., 2003; Simpson & Raubenheimer, 2005, 2012]. When consuming a low-protein diet (percentage of protein less than the mean of 19%), blue monkeys were expected to over-consume NPE to reach the protein target (in this study, ~108 kcal). The hyperbolic trend line of the observed daily NPE intakes closely tracked the hyperbolic curve generated by the expected daily NPE intakes for the protein leverage hypothesis (Figure 3.7).

Factors influencing nutritional strategy: When predicting NPE:P ratio, models with vs. without the interaction term (rank x reproductive demand) were not significantly different (LRT: X^2(df=5)=5.73, p=0.33), and I therefore dropped this interaction. The resultant full model was significantly different than a null model (LRT: X^2(df=10)=90.98, p=3.42e-15). Daily NPE:P ratio increased when the diet contained a higher percentage of fruit, when the female spent less time in the near-natural forest and when there was less ripe fruit available (Figures 3.9-3.11, Table 3.5). Young leaf availability, reproductive demand (LRT: X^2(df=5)=0.88, p=0.97), and rank had no significant effects on the NPE:P ratio. Overall, the fixed effects explained 21% of the variance and random effects did not account for additional variance.

Visual inspection of model results for the unexpected effect of ripe fruit availability indicated the possible influence of a few high NPE:P values (Figure 3.9). To explore this possibility, I removed days when a female's NPE:P ratio was >3SD from the mean NPE:P ratio (outliers=6 female-days; mean NPE:P ratio=5.2 ± 3.5). Without the outliers, the full model was still significantly different the null model (LRT: X^2(df=10)=115.92, p<2.2e-16, Table 3.5b). However, FAI ripe fruit no longer significantly related to NPE:P ratio, suggesting that those

outliers drove the significant negative relationship. The significance and direction of relationship did not change for the other predictors (Table 3.5b).

When predicting protein intake, a model with the interaction term (rank x reproductive demand) did not differ from a model without it (LRT: X^2(df=5)=4.14, p=0.53), and I again dropped the interaction. The resultant full model showed that protein intake increased with higher ripe fruit availability (Table 3.6). By contrast, rank, young leaf availability, reproductive demand (LRT: (X^2(df=5)=4.75, p=0.45), time spent in near-natural forest, and fruit in the daily diet did not have significant effects on protein intake (Table 3.6). Overall though, the full model was not significantly different from a null model with only random effects (LRT: X^2(df=10)=17. 08, p=0.07; Table 3.6).

Reproductive demand was not a significant predictor of NPE:P ratio or protein intake. However, the assumption that the demands of early gestation exceeded late lactation (so females who were simultaneously pregnant and lactating females were coded as "early gestation"), may have been incorrect. To further explore that this assumption did not mask a significant relationship between reproductive demand and nutritional strategy, I reclassified females' reproductive demands, this time separating into their own category those females with both late lactation + early gestation demands. I reran the NPE:P and protein models. Even with these changed criteria, LRTs confirmed that reproductive demand did not significantly predict NPE:P ratio, (LRT: X^2(df=6)=0.95, p=0.99) or protein intake (LRT: X^2(df=6)=4.75, p=0.58).

Rank did not predict absolute deviation from mean daily NPE:P ratio (LRT: X^2(df=1)=5.00E-03, p=0.94), or the direction of daily deviation from mean NPE:P (LRT: X^2(df=1)=3.40E-03, p=0.95; Table 3.7). Rank also did not predict absolute deviation from mean daily protein intake (LRT: X^2(df=1)=0.10, p=0.75; Table 3.7), or the direction of daily deviation

from mean protein intake (LRT: X^2(df=1)=2.60, p=0.11; Table 3.7). While rank did not predict these aspects of subjects' nutritional strategy, it did predict an aspect of subjects' feeding strategy. Specifically, rank related negatively to the number of daily unique food items (LRT: X^2(df=1)=4.28, p=0.04; Figure 3.12, Table 3.7): i.e., higher ranked females ate fewer unique food items per day than lower ranked females.

Given the results from the models testing the response variables of NPE:P ratio and absolute protein intake, one can also deduce the relationship between the predictors (reproductive demand, rank, time spent in near-natural forest, young leaf availability, ripe fruit availability, and fruit in the daily diet) and absolute NPE intake (kcal) or absolute total energy intake (kcal). Time spent in near-natural forest and fruit in the diet predicted variation in NPE:P ratio, but since those two predictors did *not* relate to change in absolute protein intake, then the variation in NPE:P ratio *must* come from variation in absolute NPE intake. Thus, time spent in near-natural forest must be negatively related to both absolute NPE and absolute total energy intakes. Likewise, fruit in the diet must be positively related to both absolute NPE and absolute total energy intakes. Following a similar logic, since neither NPE:P ratio or absolute protein intake related to young leaf availability, ripe fruit availability, reproductive demand or rank, one can deduce that absolute intakes of NPE and total energy also do not significantly relate to those predictors. Linear mixed model results (Table 3.8, 3.9) support these conclusions.

DISCUSSION

Blue monkeys prioritized protein intake and NPE:P balance, regulating their daily intake with the least amount of variation compared to other nutritional metrics. Their nutritional strategy consisted of balancing NPE to P intake in a 3.8 to 1 ratio and employing a protein

prioritization rule of compromise to approximate their mean daily intake target of 637 kcal, with 108 kcal of protein, 148 kcal of lipid, 88 kcal of NDF and 293 kcal of TNC [Chap 2]. Their average caloric percentage of protein in the diet was 19%. When protein intake was less than the average percentage, they allowed NPE:P ratio to increase, and thus to show greater variation, compared to ratios on days when protein intake was higher. A female's rank and reproductive state did not predict how much or the direction in which females deviated from mean daily NPE:P ratio or protein intake. Despite variation observed in daily NPE:P ratio, all females in the population tightly balanced *cumulative* NPE:P ratios over the study period, and were remarkably similar to one another with no evidence of a rank effect.

For *daily* NPE:P ratio, environmental factors, as well as fruit in the diet, were significant predictors: females had higher daily ratios when the diet included more fruit (measured as a percentage of calories), when they spent less time in near-natural forest, and when ripe fruit was less available. The effects of time in near-natural forest and ripe fruit availability were of comparable magnitude and direction (one standard deviation increase in the predictor led to similar decreases in the NPE:P ratio). The percentage of fruit in the daily diet, however, had a much larger effect on NPE:P: in fact, it was twice as large, and in the opposite (positive) direction. The physiological (reproductive demand) and social variables did not predict daily NPE:P ratio.

The significant negative effect of ripe fruit availability on daily NPE:P ratio was unexpected, and most likely related to outlying data points: when these outliers were removed from the dataset, ripe fruit availability was no longer a significant predictor. The outliers all represented unusual feeding days when ripe fruit was relatively unavailable and a subject consumed most (74-93%) of her calories from a single food source, either oil palm (*Elaeis sp.)*

fruits or *Bischofia javanica* fruits. Oil palm fruits are 81% lipid, 17% carbohydrate (structural and non-structural) and only 2% protein, and *B. javanica* fruit are 6 % lipid, 89% carbohydrate and <1% protein (dry weight basis, Appendix I). Thus, when females fed primarily on either of these fruits, they ingested nutrients in an unbalanced ratio with high NPE intake. Oil palm fruits were available only during periods of low overall ripe fruit availability and *B. javanica* fruit, though readily available throughout the study period, peaked in abundance during the period of low ripe fruit availability (Takahashi, unpub. data). During periods of low fruit availability, then, females may have used rare, highly prized fruit like oil palm, as well as fruit that was readily available year-round like *B. javanica*, which was eaten in proportion to its availability [Chap 2]. These results also suggest that food availability indexes are crude measures, as statistical patterns in the data may relate to the strong influence of specific species of food.

The three highest daily energetic intakes all corresponded to days on which oil palm fruit dominated the diet. The overconsumption of lipid from oil palms and resulting imbalanced NPE:P ratio does not necessarily mean that it is a poor food choice for blue monkeys. Oil palm fruits were highly selected, eaten disproportionately to their availability [Chap 2]. Behavioral observations also indicated that oil palm fruit was highly preferred: aggressive contests occurred frequently among females feeding in this tree, with low-ranking females often forced out (Takahashi, unpub. data). Also, half-eaten fruits, dropped from the tree's crown, were quickly snatched up and eaten by monkeys on the ground. Such behavior did not characterize consumption of any other fruit in the forest, indicating how much blue monkeys valued oil palm fruits. As dietary generalists, it seems they could take advantage of this rare source of fat and energy. Days on which oil palm fruit dominated the diet were extreme in the low percentage of dietary protein. Over the course of the study period, though, all individuals balanced cumulative

NPE:P intake in remarkably tight ratios. Overall, then, despite days of feasting on fat from oil palm fruits, blue monkeys adhered to their nutritional strategy of balancing NPE:P, reinforcing the idea that nutrient balancing was the optimal way to reach their target intakes.

For factors affecting protein intake, while the model indicated a positive relationship with ripe fruit availability, the overall model was not an improvement on a null model. I therefore conclude that the factors (daily time in near-natural forest, fruit in diet) that predicted daily NPE:P ratio did not relate to protein intake. This finding agreed with the overall picture that regardless of environmental, social, or physiological differences, all females in the population prioritized consuming their target protein intake. Females seem to allow less variation in protein intake than NPE:P ratio.

Blue monkeys resembled other primates in balancing consumption of NPE and P, and the NPE:P ratio of 3.8 was on the lower end of the range reported for other omnivorous species. For example, a South African baboon (*Papio hamadryas ursinus)* exhibited a 5:1 ratio while humans in an experimental setting showed a ratio of ca. 6:1 [Simpson et al., 2003; Simpson & Raubenheimer, 2005; Johnson et al., 2013]. Black howler monkeys, while traditionally categorized as folivores, ate substantial amounts of fruit and balanced a ratio of 5.3 [Martínez-Mota et al., 2016]. The two lowest ratios currently available come from mainly folivorous species: 2:1 to 3:1 in mountain gorillas (*Gorilla beringei* [Rothman et al., 2011b]) and 1.6:1 in guerezas (*Colobus guereza* [Johnson et al., 2017]). The two highest ratios were recorded for one predominately frugivorous species and, interestingly, one primate that is traditionally considered a folivore but also consumes large amounts of fruit: 8:1 in spider monkeys (*Ateles chamek* [Felton et al., 2009b; 2009c]) and 9.5:1 in diademed sifakas (*Propithecus diadema* [Irwin et al., 2015]). The emerging pattern suggests that primates generally balance NPE:P, despite a wide

range of diets, from frugivory to omnivory to folivory. The exact ratio, though, seems to vary by species, with higher ratios in more frugivorous species, as expected when the diet incudes sugary (high TNC) fruits. Information on primates that specialize in insectivory and gumnivory would be important to confirm this primate-wide pattern.

When the target diet was not achievable, blue monkeys prioritized protein intake. This rule of compromise appears to predominate in primates. Humans, spider monkeys (*Ateles chamek*), black howler monkeys (*Aloutta pigra*), and sportive lemurs (*Lepilemur leucopus*) all show this rule [Simpson et al., 2003; Simpson & Raubenheimer, 2005, 2012; Felton et al., 2009b; Amato & Garber, 2014; Dröscher et al., 2016; Martínez-Mota et al., 2016; Raubenheimer & Simpson, 2016]. The body cannot store amino acids from protein, unlike components from other nutrients, so shortfalls in protein may be particularly harmful. One study (on black howler monkeys) showed that lower protein intakes related to elevated glucocorticoid hormones, whereas fluctuations in total daily energy intake did not [Martínez-Mota et al., 2016]).

Protein prioritization, however, does not seem to be the only rule of compromise seen in primates. For example, gorillas (*Gorilla beringei*) prioritized NPE rather than protein intake, over-consuming protein to do so [Rothman et al., 2011]. For large-bodied folivores like gorillas, it may be that protein, which is relatively abundant in young leaves, is less of a concern than NPE, which may be relatively low in their fibrous diet. In another example, Verreaux's sifakas (*Propithecus verreauxi*) seemed to use overall nutrient intake reduction as their rule of compromise, thus maintaining the same NPE:P balance across seasons [Irwin et al., 2015]. Finally, there is some evidence that Javan slow lorises (*Nycticebus javanicus*) prioritize lipid intake across seasons [Cabana et al., 2017]. Overall, it seems that while all primates studied thus far show evidence of balancing NPE:P, the rules of compromise may not be universal.

Daily nutritional strategy was more closely related to environmental factors and diet composition than social or physiological factors. Females that spent less time in the near-natural forest had higher NPE:P ratios. When feeding in farm/plantation and village forests, blue monkeys focused on *Psidium guajava* and *Bischofia javanica* fruit, two food resources high in TNC, resulting in higher NPE:P ratios. The second biggest category of food, protein-rich young leaves, came mainly from the near-natural forest, so monkeys feeding there consumed more protein and had a lower NPE:P ratio.

The influence of outliers on the relationship between ripe fruit availability and NPE:P ratio suggests that ripe fruit availability may not generally relate to nutrient balancing, except for exceptional feeding days when particular fruits dominate the diet. In contrast, results from Chapter 2 indicated that fruit availability (not only ripe) related positively to fruit in the diet (absolute caloric intake and % of caloric diet), and this chapter showed that fruit in the diet (by percentage of kcal) was positively related to NPE:P ratio (most likely because of high sugar levels in fruits). So, it may be that nutritional balancing of blue monkeys responds to overall fruit availability, but not ripe fruit availability. However, fruit availability does not seem to relate to absolute intake of NPE or protein [Chap 2].

Other studies have generally also found positive relationships among fruit availability, fruit consumption, and nutrient intake and even nutrient balancing. For example, when seasonal fruits were more available, Ugandan gorillas ate a fruit heavy diet with a mean NPE:P ratio of 3:1, which was higher than the ratio they achieved (2.1) during the season when the leaves dominated the diet [Rothman et al., 2011]. Sifakas also showed higher nutrient (NPE, crude protein and fat) and energy intake during seasons of high food availability, especially fruit [Koch et al., 2017]. For female orangutans, greater fruit availability also coincided with an increase in

total energy intake, but a decrease in protein intake [Vogel et al., 2017]. And finally, spider monkeys' diets fluctuated in NPE amount in response to amount of ripe fruit in the diet [Felton et al., 2009b], but black howler monkeys' diets decreased in energy content with increasing percentage of fruit in the diet [Amato & Garber, 2014]. Across primates, nutrient intake and NPE:P ratio seem to change in response to fruit in the diet and its availability, though the exact nutrients and direction of change varies.

One social factor, dominance rank, related to feeding strategy but not nutritional strategy in blue monkey females. Specifically, higher ranked females ate fewer unique food items each day than lower ranked females. Only one other study examined rank effect on dietary breadth in *C. mitis*: adult females in a South African population showed no relationship between rank and annual dietary breadth [Payne et al., 2003]. In terms of nutritional strategy, rank had no effect on daily or cumulative NPE:P ratio or deviation from mean daily NPE:P ratio, even though Foerster et al. [2011] reported that high-ranked females have priority of access to fruits. Similarly, rank had no effect on daily protein intake and no effect on deviation from mean protein intake. It is possible that low-ranked females employed behavioral strategies, such as increasing daily dietary breadth, to cope with social constraints when feeding, and thus avoided changes in protein or NPE:P ratio. Although blue monkeys are group-living and female-bonded, group members often spread out over several hundred meters, and occasionally form sub-groups that are separated by more than 0.5 km. The facts that females often feed alone in a tree, that most feeding trees could accommodate additional individuals [Cords, 2002a], and that alternative food sources are usually in close proximity to one another, suggests that individual females face few constraints in choosing what to eat, even if low-ranking.

The fact that rank affected only one of several dietary or nutritional variables tested in this study agrees with other reports from *C. mitis* that mostly failed to find rank-based advantages in feeding behavior (i.e. time spent feeding, proportion of time feeding of different food types, fruit intake rate, plant species eaten, number of food species) or reproduction (probability of conception, and successful offspring production rate (infants survive to 1 year [Cords, 2000, 2002b; Payne et al., 2003; Pazol & Cords, 2005; Roberts & Cords, 2013]. The few rank-based fitness-related advantages known so far from equatorial populations are that higher ranking females (1) receive agonism at lower rates [Klass & Cords 2015], (2) have preferential access to fruits, (3) have lower glucocorticoid hormones when lactating [Foerster et al., 2011], and (4) have lower probability of infection, egg count, and richness of gastrointestinal helminth parasites [Foerster et al., 2015] than lower ranked females. In another sub-species in more temperate coastal dune forest, Payne et al. [2003] reported that higher ranked females showed less monthly variation in proportion of feeding records allocated to fruit than lower ranked females [Payne et al., 2003].

I found no evidence that reproductive demand related to the nutritional strategy of female blue monkeys. Fluctuations in glucocorticoid hormones suggest seasonal energetic deficits in females that are in late pregnancy and early lactation relative to those in other reproductive states [Foerster et al., 2012]. Though reproductive females may be energetically challenged during periods of low food availability, this study suggests they are able, nonetheless, to meet dietary needs and maintain an average NPE:P ratio and protein intake. Consistent intake and strategy, regardless of reproductive demand, suggests that blue monkeys may follow a capital breeding strategy, relying more on stored reserves in the body than current intake [Janson & Verdolin, 2005]. Further, reproduction may have less of an effect on energy and nutritional needs than

previously thought. Emerging research on total energy expenditure in primates indicates that it is largely determined by basal metabolic rate and there is little variation because of reproduction [Pontzer, 2015]. For example, female humans in traditional farming communities, with high physical demands, may reduce basal metabolic rate and mobilize fat reserves to offset the costs of reproduction while keeping total energy expenditure within a narrow range. On an evolutionary scale, blue monkeys may be able to cope with their reproductive demands, without consequence to their nutritional strategy, because they have evolved a relatively long inter-birth interval [Cords, 2012]. Slowing down the reproductive rate may ensure that females have the body reserves upon which to draw without consuming more nutrients or energy. Moreover, fruit availability did not relate to glucocorticoid hormones [Foerster et al., 2012] which suggests that Kakamega Forest may be a relatively permissive landscape, lacking large fluctuations in nutrient or energy availability that might cause deviations from the nutritional balance in other more extreme habitats. By contrast, sifakas live in seasonally extreme habitat and females during the late stage of lactation had higher food intake (and thus higher intake of protein, fat, TNC, and overall energy) compared to females in other reproductive stages and males [Koch et al., 2017]. In an opposite way, spider monkeys live in forests that are less variable climatically, and there were no significant between-sex differences in nutrient intake or composition, suggesting that the females (all pregnant or lactating) consumed enough energy and macronutrients to meet reproductive needs [Felton et al., 2009b]. Similarly, female black howler monkeys, also living in a relatively less extreme climate, did not show a relationship between reproductive demands and total daily energy intake or fecal glucocorticoids [Martínez-Mota et al., 2016]. While it is inarguable that reproduction poses an energetic and nutritional demand on female primates, that

demand may affect nutritional intake (and possibly nutritional strategy) most in environments with extreme climatic fluctuations.

In summary, the results indicate both a short- and long-term pattern in nutritional strategy for blue monkeys in the study population. On a daily basis, females prioritized protein intake, regardless of potential influences from social, environmental or physiological factors. Females balanced daily NPE:P intake to a lesser extent, taking advantage of high NPE foods like oil palm and *Bischofia javanica* fruit. On a longer term basis (i.e. over the 8 months of data collection), however, females tightly balanced cumulative NPE:P intake, regardless of daily fluctuations in NPE:P ratio that were linked to habitat use and diet. This long-term pattern in all 24 subjects suggests that it a species-typical strategy, though follow-ups in other populations would be necessary for confirmation. By evaluating how multiple factors influence the nutritional strategy of blue monkeys, I showed that blue monkeys are generalist feeders, exercising flexibility to navigate heterogeneous landscapes, social constraints, and reproductive demands without deviating from a specific nutritional strategy. Potential deviations (e.g. those caused by reproductive demand or rank) may have been mitigated by evolved solutions such as a relatively slow reproductive rate and behavioral adjustments, such as avoidance of within-group feeding competition by spreading out. Finally, the pattern of NPE:P balancing seen in many studies of primate nutritional ecology, including this one, suggests that the diverse dietary strategies of primates may have evolved to allow them to adhere to a balance of NPE:P.

CHAPTER 3. TABLES AND FIGURES

Table 3.1. Study groups' size (mean for all members, January 24-September 25, 2015), home range size, and habitat composition. Home range based on GPS movements of study subjects during study period (see Chap. 2 for details). Final three columns show the percentage composition of the home range by the three different habitat types. Table is ordered by increasing group size.

Group name	Group size	Home range	% farm/plantation forest	% near-natural forest	% village forest
GN	31	23.9 ha	--	92.1	7.9
GSC	55	41.8 ha	44.4	55.6	--
TWS	62	52.3 ha	2.2	85.2	12.6

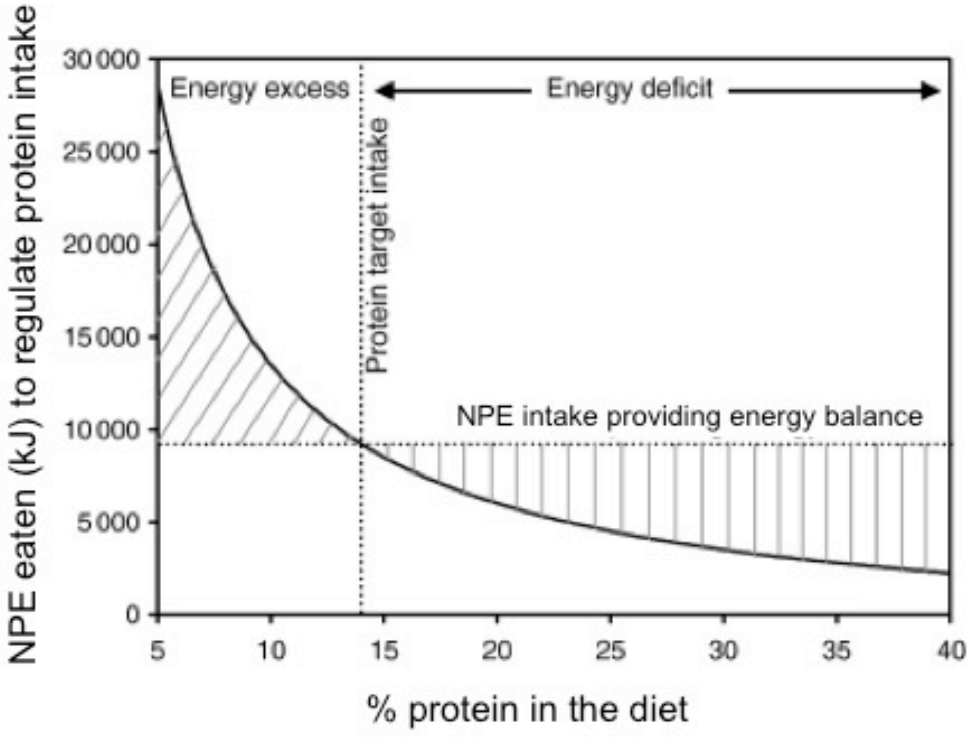


Figure 3.1. Protein leverage hypothesis. Figure copied from [Simpson & Raubenheimer, 2005]. The protein leverage hypothesis states that if protein intake is prioritized, the percentage of protein in the diet will determine the amount of NPE consumed. Even more, the target protein intake (vertical dashed line) demarcates when animals will be in energy excess or deficit. When the protein percentage falls to the left of the target intake, even slight deviations will lead the animal to greatly over-consume NPE (diagonally hashed area). When the protein percentage falls to the right of the target intake, the animal will under-consume NPE (vertically hashed area).

Table 3.2. Mean and SD of variables used as fixed effects in linear mixed models that predicted NPE:P ratio and protein intake (kcal). These variables were standardized in the linear mixed models.

Fixed effect	Mean	SD	N
proportion of time in near-natural forest	0.70	0.32	371 female-days
percentage of fruit in daily diet (kcal)	56.24	26.28	371 female-days
FAI ripe fruit	4330.65	3308.81	48 group-FAI scores
FAI young leaves	40239.26	8276.26	48 group-FAI scores
rank	0.51	0.35	24 subjects

Table 3.3. Variation in daily intake of energy and nutrients. Table ordered by increasing CV of mean. Food includes dry weight of protein, lipid, TNC, NDF, and ash. Total energy includes caloric sum of protein, lipid, TNC, and NDF. NPE:P ratio calculated by dividing sum of lipid, TNC and NDF (kcal) by the caloric value of protein (kcal).

	Mean (N=371 female-days)			Grand mean (N=24 subjects)		
	Mean	SD	CV	Mean	SD	CV
Protein (kcal)	107.87	53.10	0.49	107.84	12.86	0.12
Food (g)	226.17	123.43	0.55	226.45	38.33	0.17
NDF (kcal)	87.99	51.09	0.58	88.10	17.55	0.20
TNC (kcal)	293.02	177.76	0.61	293.34	46.91	0.16
NDF (g)	93.43	57.18	0.61	93.66	22.33	0.24
Total energy (kcal)	636.95	414.58	0.65	637.09	104.67	0.16
NPE:P	5.17	3.51	0.68	5.18	0.86	0.17
NPE (kcal)	529.08	384.28	0.73	529.25	97.34	0.18
Lipid (kcal)	148.07	271.99	1.84	147.81	72.41	0.49

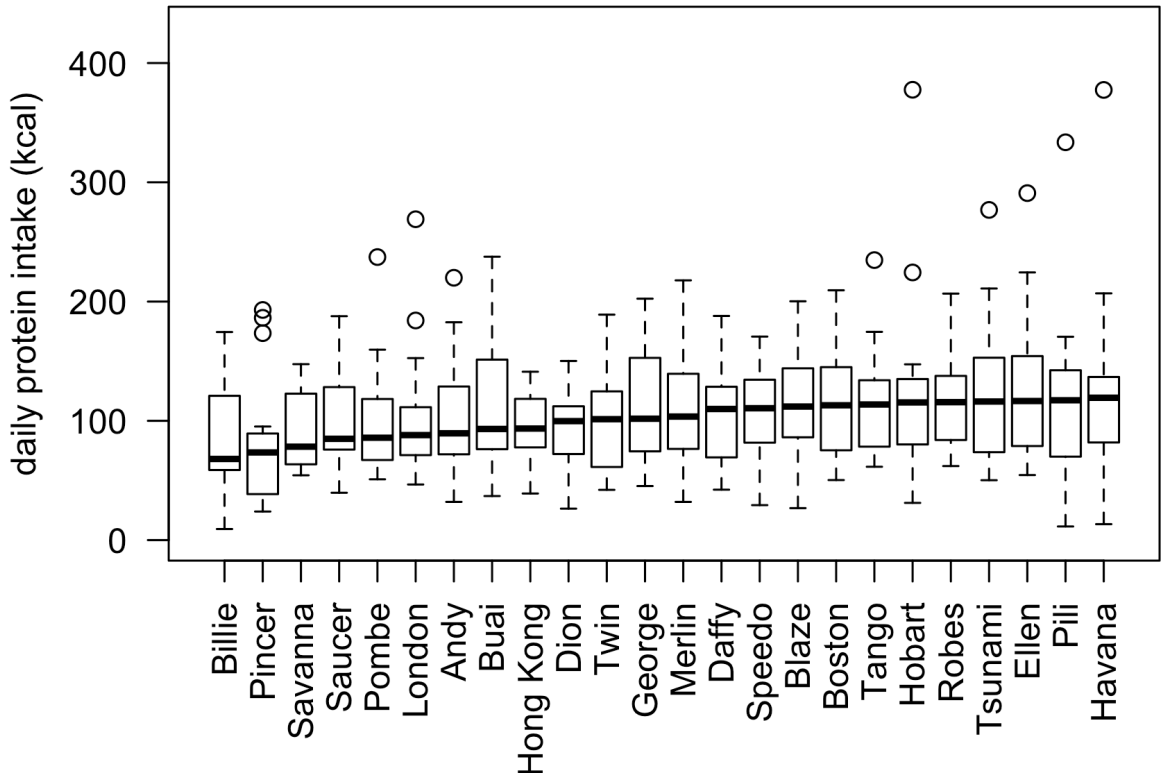


Figure 3.2. Variation in individuals' daily intake of protein (kcal). Individuals are arranged in ascending order of median daily protein intake (kcal). N=15-16 days per female. Boxplots show median and interquartile range. Whiskers represent the most extreme data point, no more than 1.5 * IQR away from the box. Outliers are data points beyond the whiskers.

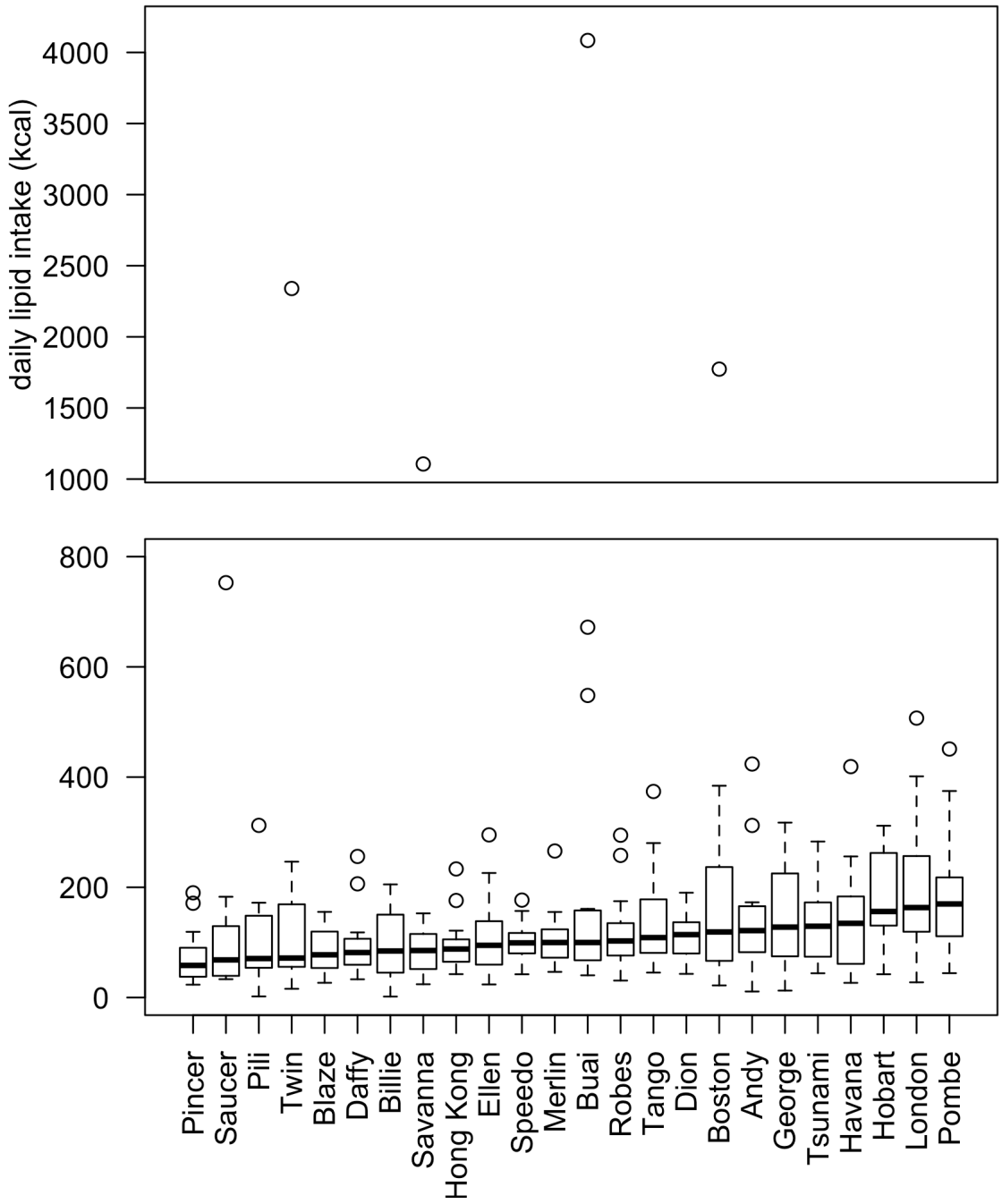


Figure 3.3. Variation in individuals' daily intake of lipid (kcal). Individuals are arranged in ascending order of median of daily lipid intake (kcal). N=15-16 days per female. See Figure 3.2 for boxplot explanation.

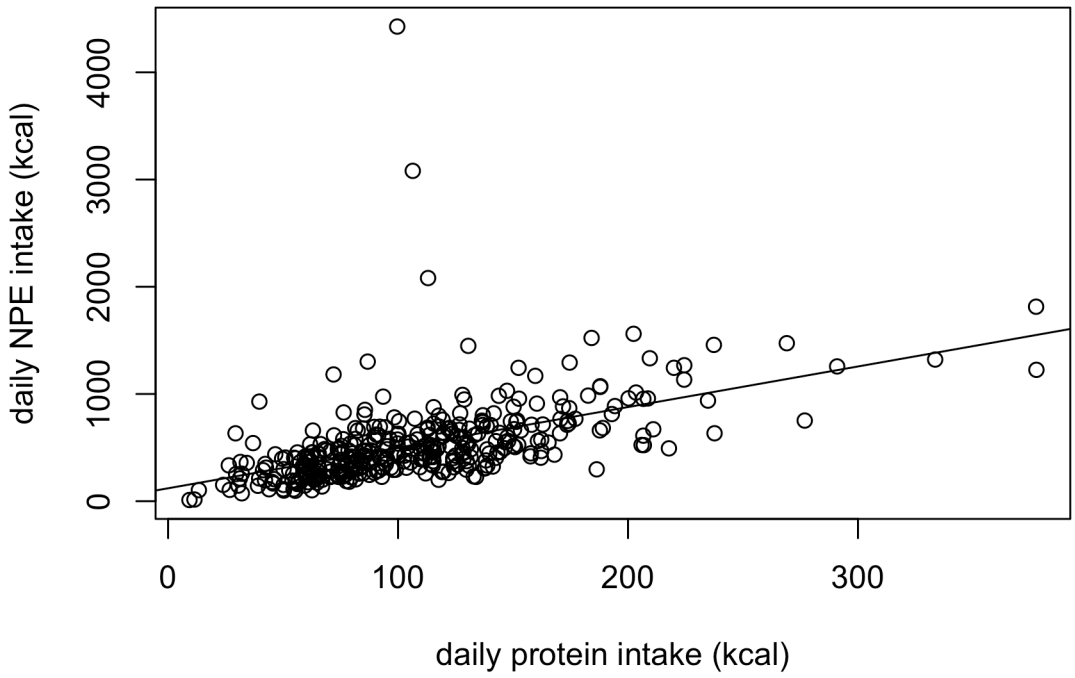
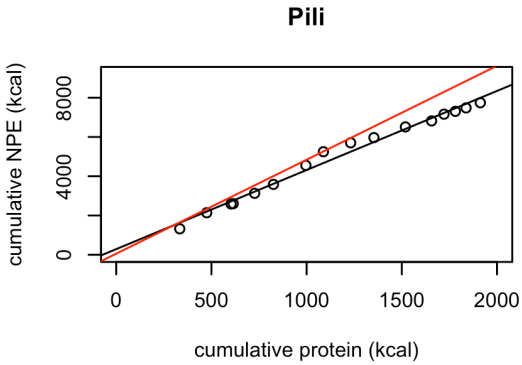


Figure 3.4. Relationship between NPE and protein intake, N=371 female-days. Daily protein intake correlates positively and significantly with daily NPE intake (black line shows predicted slope of protein intake and intercept of linear mixed model).

Table 3.4. OLS regression model statistics for subjects' relationships between cumulative NPE and cumulative P. N=15-16 female-days for each subject. Females within groups are ordered by rank.

	Subject	β	SE	95% CI		t value	p value	R^2
GN	Pili	4.03	0.13	3.76	4.30	31.47	2.15E-14	0.99
	Pincer	4.54	0.17	4.17	4.92	25.99	3.01E-13	0.98
	Merlin	4.21	0.15	3.88	4.53	27.68	1.27E-13	0.98
	Tango	5.85	0.22	5.38	6.31	27.09	8.03E-13	0.98
	Speedo	4.50	0.11	4.26	4.74	40.71	4.28E-15	0.99
	Robes	4.75	0.10	4.54	4.97	47.75	<2e-16	0.99
	Daffy	4.51	0.09	4.33	4.70	51.98	<2e-16	1.00
	Dion	5.24	0.12	4.98	5.50	43.36	1.89E-15	0.99
TWS	Twin	6.71	0.39	5.88	7.53	17.36	7.27E-11	0.96
	Saucer	4.34	0.12	4.09	4.59	37.64	1.17E-14	0.99
	Savanna	4.65	0.15	4.32	4.98	30.13	3.92E-14	0.98
	Boston	4.98	0.21	4.52	5.44	23.23	5.70E-12	0.98
	Billie	4.74	0.08	4.57	4.92	58.00	<2e-16	1.00
	Buai	5.96	0.60	4.66	7.25	9.87	1.10E-07	0.87
	Blaze	4.03	0.09	3.84	4.21	46.55	7.56E-16	0.99
	Ellen	4.41	0.07	4.27	4.56	66.34	<2e-16	1.00
GSC	Andy	5.17	0.06	5.03	5.30	82.88	<2e-16	1.00
	George	4.71	0.10	4.49	4.92	46.96	<2e-16	0.99
	Pombe	6.15	0.05	6.05	6.24	135.50	<2e-16	1.00
	London	6.62	0.12	6.37	6.88	56.18	<2e-16	1.00
	Havana	4.13	0.07	3.99	4.27	63.12	<2e-16	1.00
	Hobart	4.77	0.11	4.53	5.01	43.15	2.01E-15	0.99
	Hong Kong	4.98	0.16	4.64	5.32	31.34	1.24E-13	0.99
	Tsunami	4.60	0.11	4.36	4.83	41.59	4.52E-16	0.99

a) GN group


Pili
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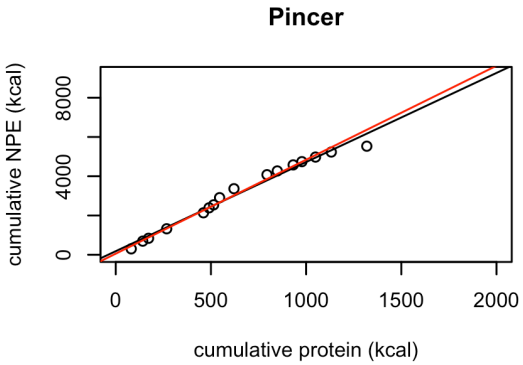
0
4000
8000
0
500
1000
1500
2000
cumulative protein (kcal)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cumulative NPE (kcal)
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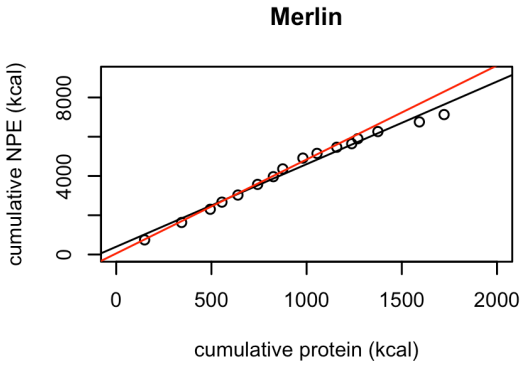
8000
0
500
1000
1500
2000
cumulative protein (kcal)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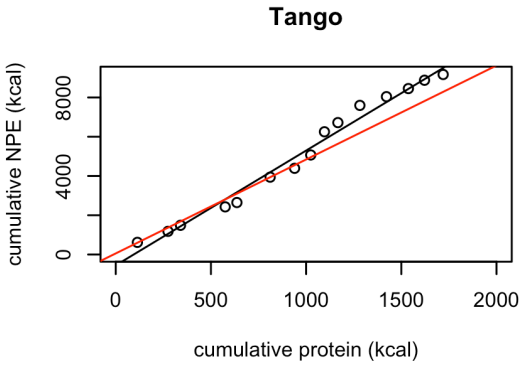
2000
cumulative protein (kcal)


Tango
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0
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1000
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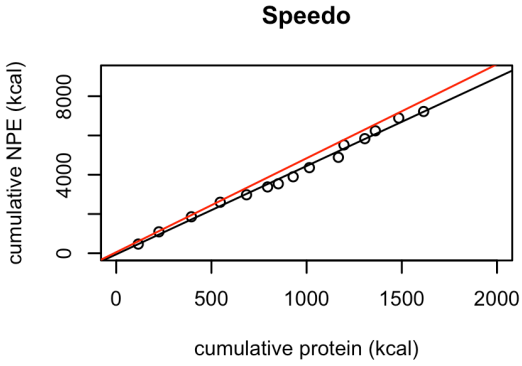
2000
cumulative protein (kcal)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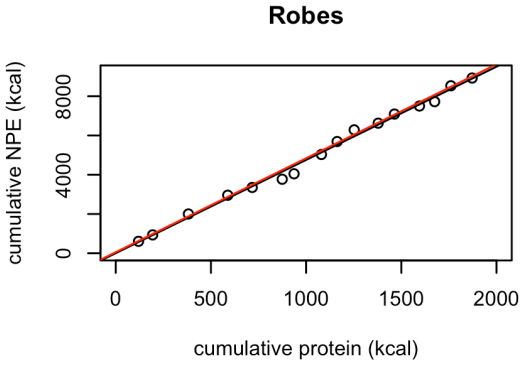
2000
cumulative protein (kcal)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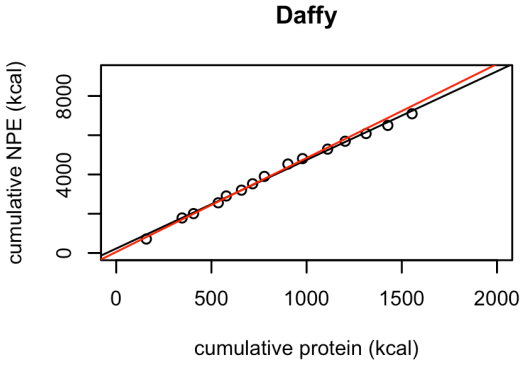
1500
2000
cumulative protein (kcal)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cumulative NPE (kcal)
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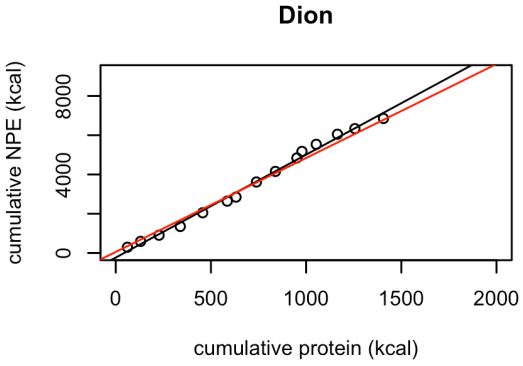
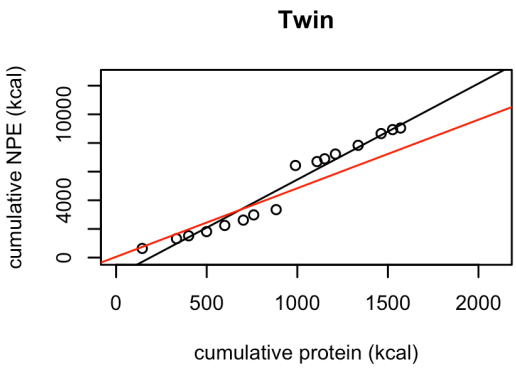
0
500
1000
1500
2000
cumulative protein (kcal)


Dion
cumulative NPE (kcal)
0
4000
8000
0
500
1000
1500
2000
cumulative protein (kcal)

b) TWS group


Twin
cumulative NPE (kcal)
0
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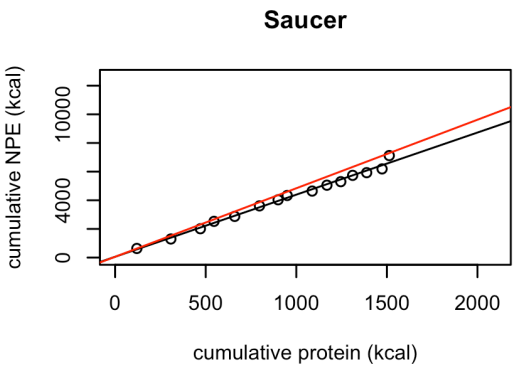
10000
0
500
1000
1500
2000
cumulative protein (kcal)


Saucer
cumulative NPE (kcal)
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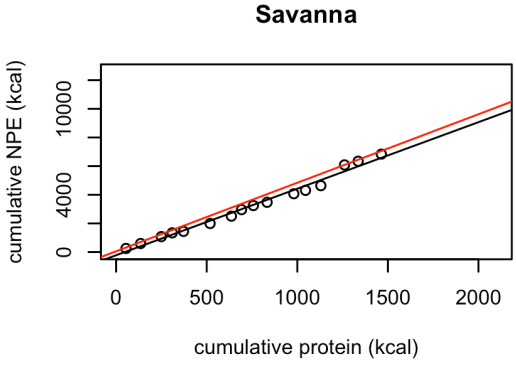
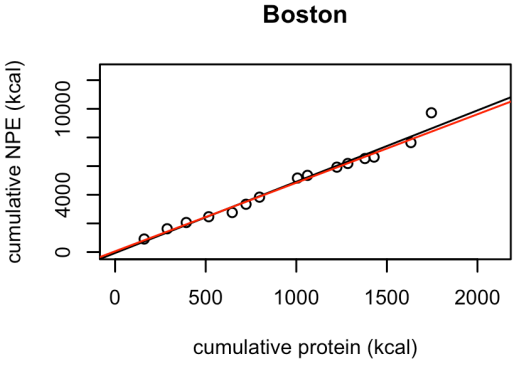
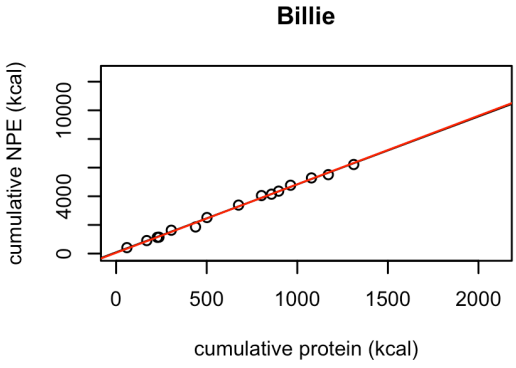
10000
0
500
1000
1500
2000
cumulative protein (kcal)


Savanna
cumulative NPE (kcal)
0
4000
10000
0
500
1000
1500
2000
cumulative protein (kcal)


Boston
cumulative NPE (kcal)
0
4000
10000
0
500
1000
1500
2000
cumulative protein (kcal)


Billie
cumulative NPE (kcal)
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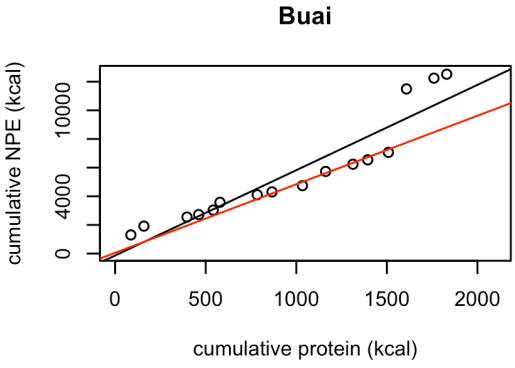
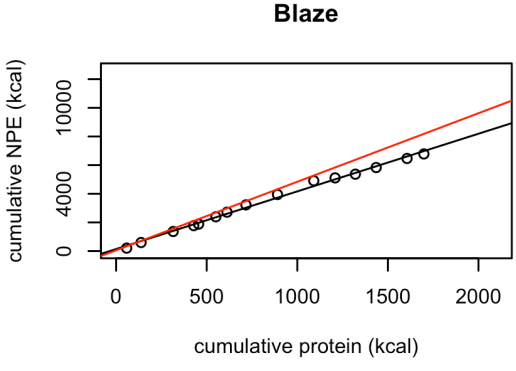
4000
10000
0
500
1000
1500
2000
cumulative protein (kcal)


Buai
cumulative NPE (kcal)
0
4000
10000
0
500
1000
1500
2000
cumulative protein (kcal)


Blaze
cumulative NPE (kcal)
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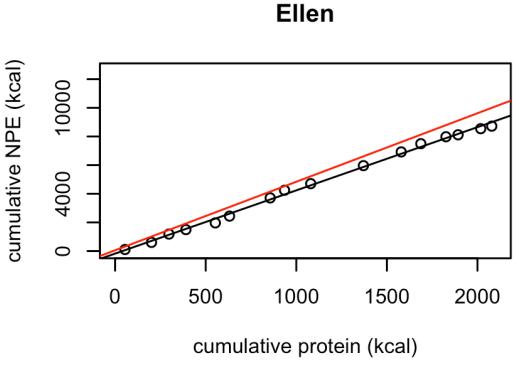
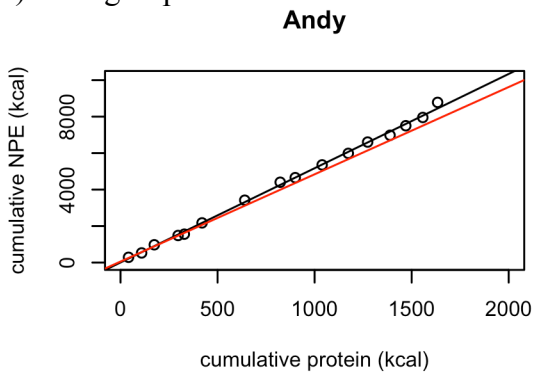
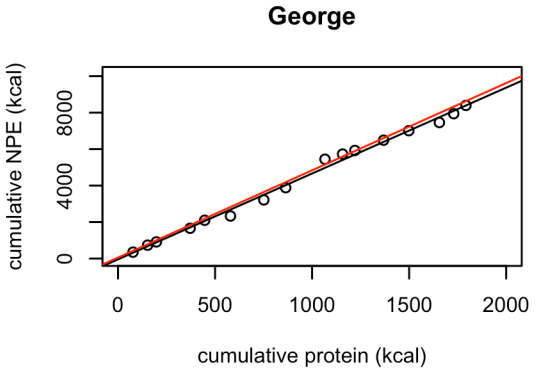
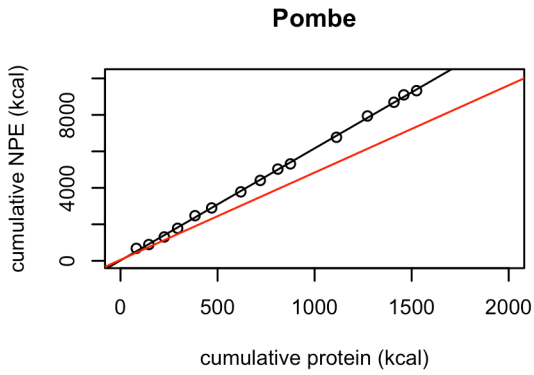
0
500
1000
1500
2000
cumulative protein (kcal)

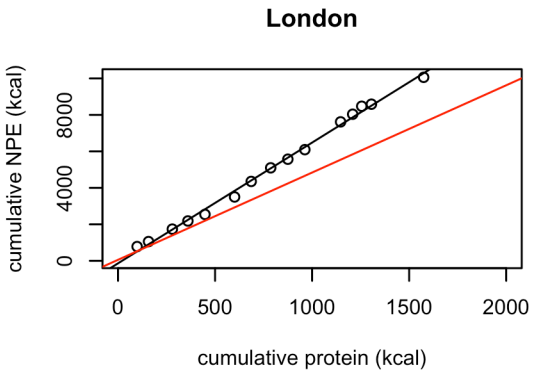

Ellen
cumulative NPE (kcal)
0
4000
10000
0
500
1000
1500
2000
cumulative protein (kcal)

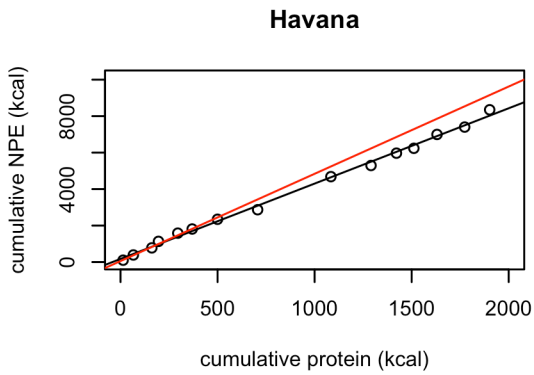
c) GSC group

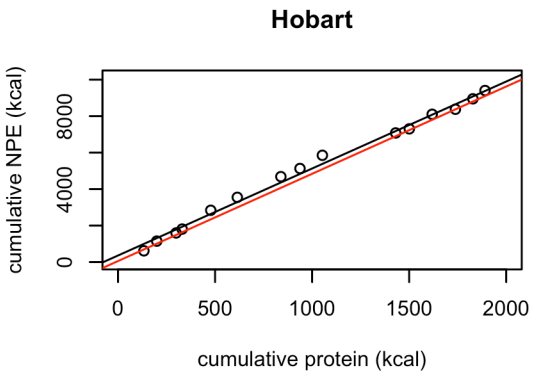

Andy
cumulative NPE (kcal)
0
4000
8000
0
500
1000
1500
2000
cumulative protein (kcal)

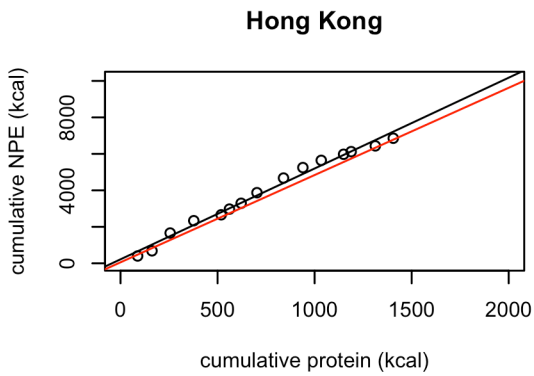

George
cumulative NPE (kcal)
0
4000
8000
0
500
1000
1500
2000
cumulative protein (kcal)


Pombe
cumulative NPE (kcal)
0
4000
8000
0
500
1000
1500
2000
cumulative protein (kcal)


London
cumulative NPE (kcal)
0
4000
8000
0
500
1000
1500
2000
cumulative protein (kcal)


Havana
cumulative NPE (kcal)
0
4000
8000
0
500
1000
1500
2000
cumulative protein (kcal)


Hobart
cumulative NPE (kcal)
0
4000
8000
0
500
1000
1500
2000
cumulative protein (kcal)


Hong Kong
cumulative NPE (kcal)
0
4000
8000
0
500
1000
1500
2000
cumulative protein (kcal)

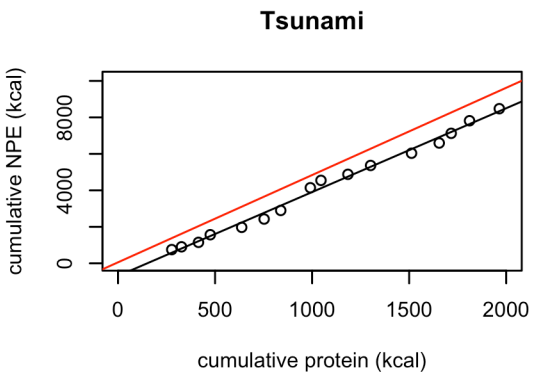

Tsunami
cumulative NPE (kcal)
0
4000
8000
0
500
1000
1500
2000
cumulative protein (kcal)

Figure 3.5. Cumulative NPE:P balancing for individuals in three study groups. Points are cumulative daily intakes (recalculated for each observation day). Black lines represent OLS regressions for individuals. Red lines represent OLS regressions for the group. Individuals are ordered by dominance rank (by row, with highest in top left corner to lowest in bottom right corner) in each group (a, b, c).

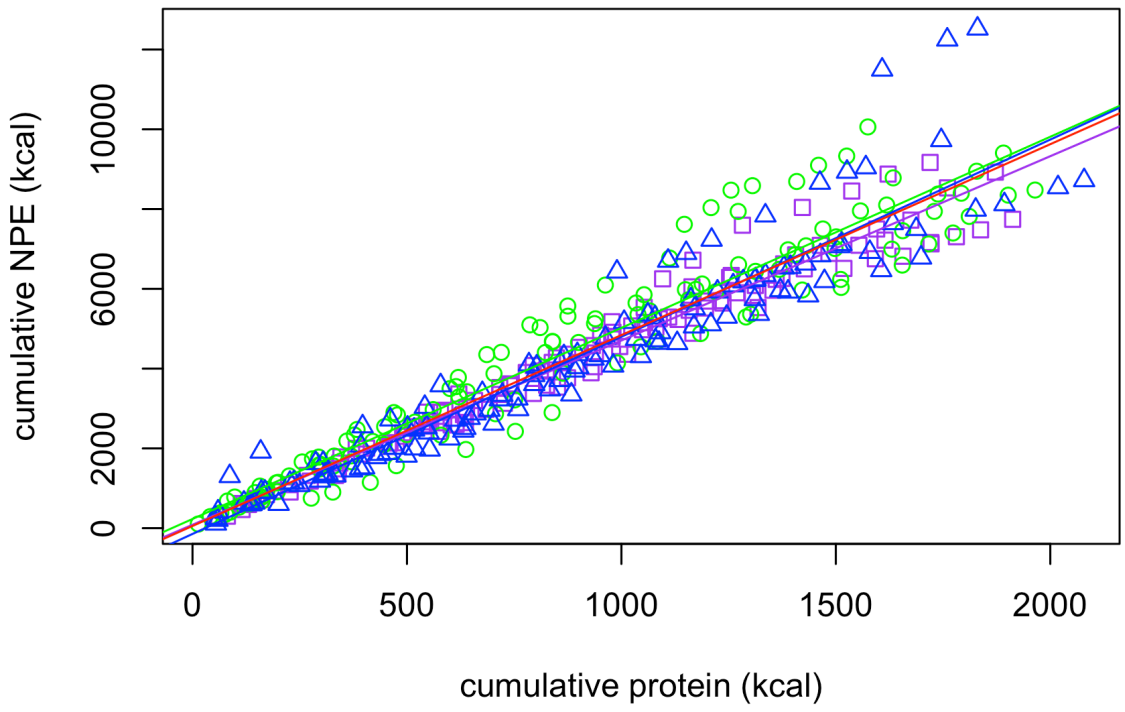


Figure 3.6. Relationship between cumulative NPE and cumulative protein intake (kcal). Each point represents a cumulative daily intake for one individual (N=15-16 female-days for each of 24 subjects). Purple squares=GN group, green circles=GSC group, blue triangles=TWS group. Matching colored lines show OLS linear relationship by group. Red line shows OLS regression for population.

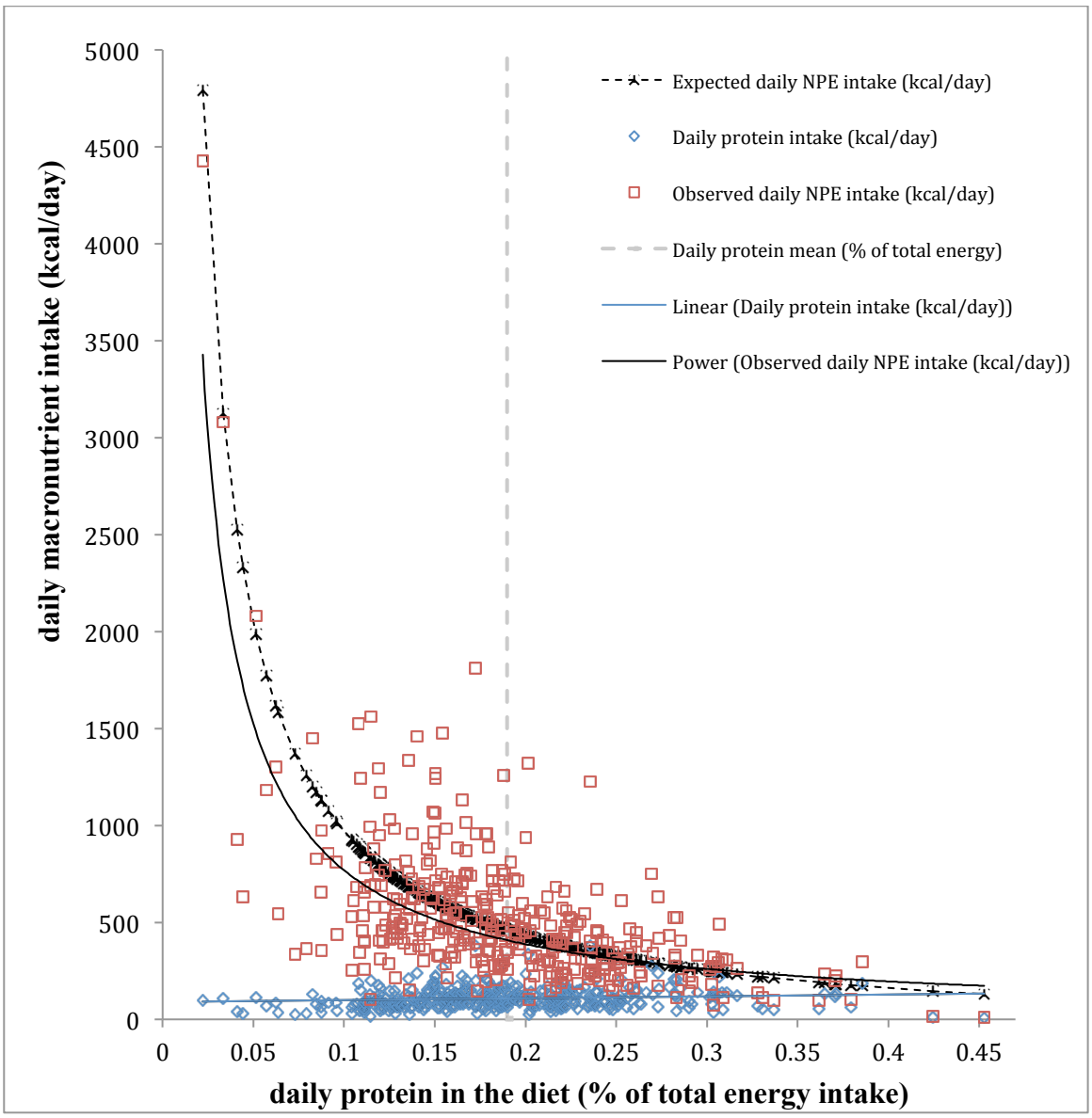


Figure 3.7. Protein leverage in diets of blue monkeys. Blue diamonds represent daily protein intake (kcal/day). Red squares represent observed daily NPE intake (kcal/day). Black hashes, connected with hyperbolic dashed line, represent expected daily NPE intake (kcal/day) if protein intake was tightly regulated. Hyperbolic solid line represents power regression for points representing observed daily NPE intake ($y=79.20x^{-0.99}$, $R^2=0.35$). Blue horizontal solid line represents linear regression for points representing observed daily protein intake ($y=95.71x + 89.84$, $R^2=0.01$).

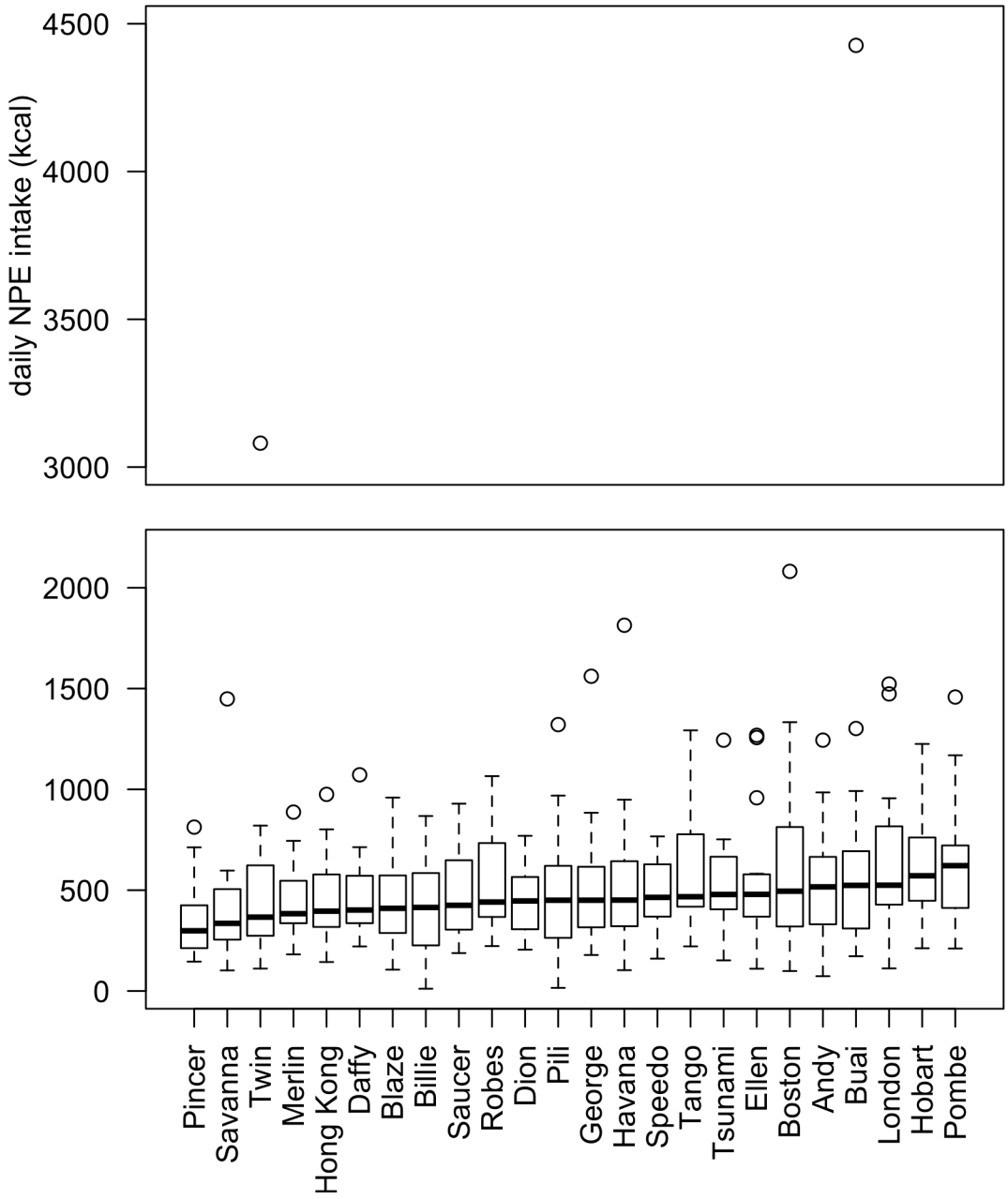


Figure 3.8. Variation in individuals' daily intake of non-protein energy (kcal). Individuals are arranged by median daily intake (kcal). N=15-16 days per female. See Figure 3.2 for boxplot explanation.

Table 3.5. Linear mixed models predicting NPE:P ratio for a) all data and b) data excluding outliers (>3SD from the mean NPE:P ratio). Subject ID nested in Group were included as random effects. All continuous fixed effects were standardized z-scores. For reproductive demand, "none" was the reference class. * indicates significance ($p<0.05$).

Fixed effect	Estimate	SE	95% CI		df	t-value	p-value
a) all data (N=371 female-days)							
FAI ripe fruit*	-0.72	0.20	-1.10	− -0.33	360	-3.62	3.33E-04
Proportion of daily time in near-natural forest*	-0.72	0.20	-1.12	− -0.33	360	-3.55	4.38E-04
Percentage fruit in the daily diet*	1.48	0.18	1.14	− 1.83	360	8.37	1.33E-15
Rank	-0.02	0.17	-0.35	− 0.31	360	-0.10	0.92
FAI young leaves	-0.08	0.18	-0.43	− 0.26	360	-0.46	0.64
Reproductive demand (none)							
early gestation	0.03	0.69	-1.31	− 1.38	360	0.05	0.96
late gestation	-0.04	0.75	-1.50	− 1.42	360	-0.05	0.96
early lactation	-0.26	0.59	-1.40	− 0.87	360	-0.45	0.65
mid lactation	-0.41	0.78	-1.92	− 1.10	360	-0.53	0.60
late lactation	-0.35	0.58	-1.48	− 0.77	360	-0.61	0.54
Intercept*	5.39	0.49	4.43	− 6.34	360	10.92	< 2.00E-16
b) data excluding outliers (N=365 female-days)							
FAI ripe fruit	-0.19	0.12	-0.38	− 0.06	21.00	-1.60	0.12
Proportion of daily time in near-natural forest *	-0.40	0.12	-0.65	− -0.21	34.20	-3.35	1.97E-03
Percentage fruit in the daily diet *	0.98	0.10	0.79	− 1.17	352.00	9.80	< 2e-16
Rank	-0.01	0.10	-0.20	− 0.17	352.20	-0.15	0.88
FAI young leaves	0.10	0.13	-0.11	− 0.27	1.40	0.77	0.55
Reproductive demand (none)							
early gestation	0.20	0.39	-0.55	− 0.98	353.70	0.52	0.60
late gestation	0.18	0.43	-0.66	− 0.99	351.00	0.43	0.67
early lactation	0.11	0.33	-0.54	− 0.74	353.50	0.35	0.73
mid lactation	0.20	0.44	-0.67	− 1.02	345.30	0.45	0.65
late lactation	-0.03	0.33	-0.66	− 0.60	353.30	-0.10	0.92
Intercept*	4.75	0.29	4.22	− 5.29	10.30	16.20	1.15E-08

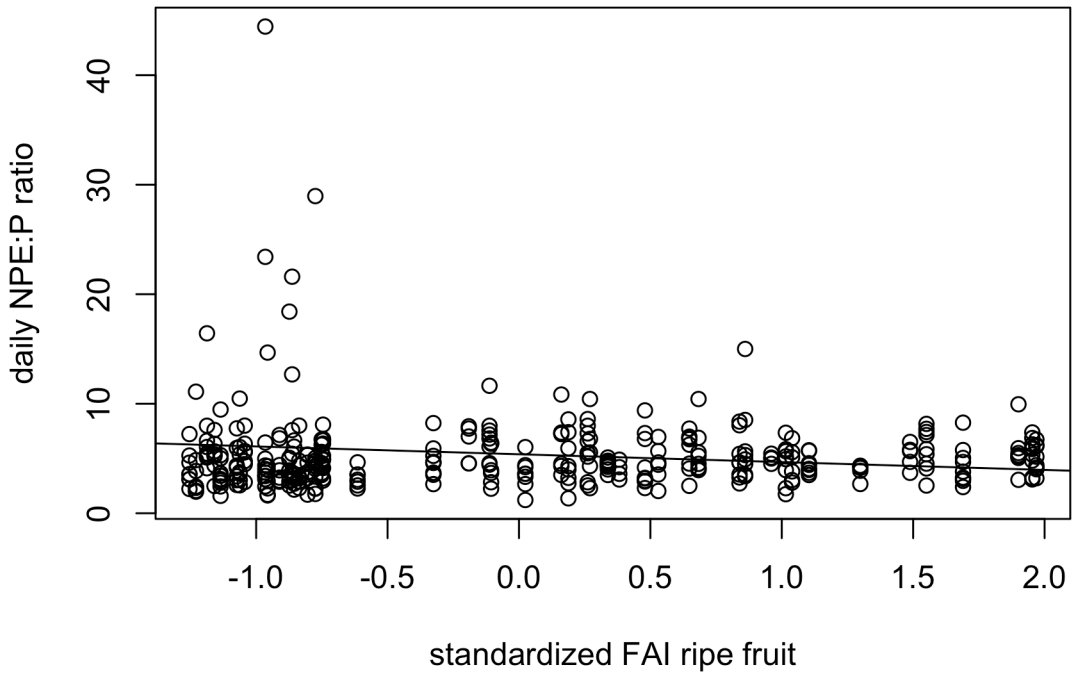


Figure 3.9 Negative relationship between NPE:P ratio and standardized FAI ripe fruit. Each point represents a daily NPE:P ratio (N=371). Black line based on slope and intercept of linear mixed model.

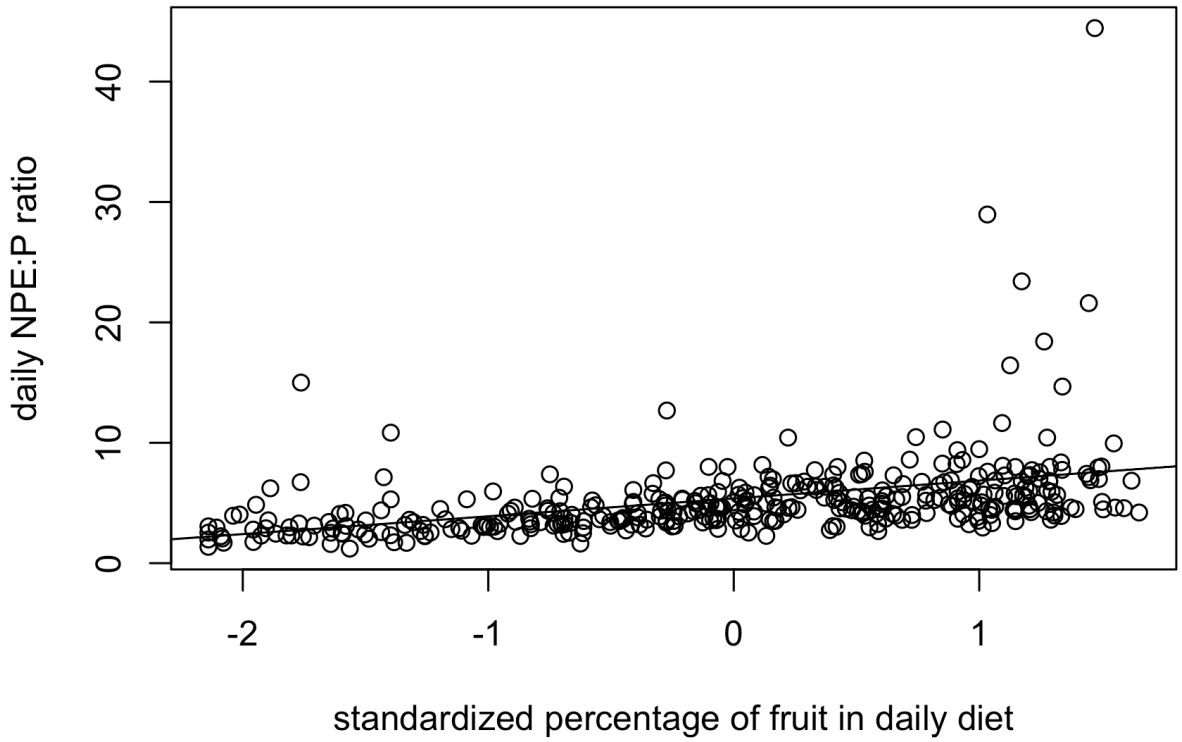


Figure 3.10. Positive relationship between NPE:P ratio and standardized percentage of fruit in daily diet. Each point represents a daily NPE:P ratio (N=371). Black line based on predicted slope and intercept of linear mixed model.

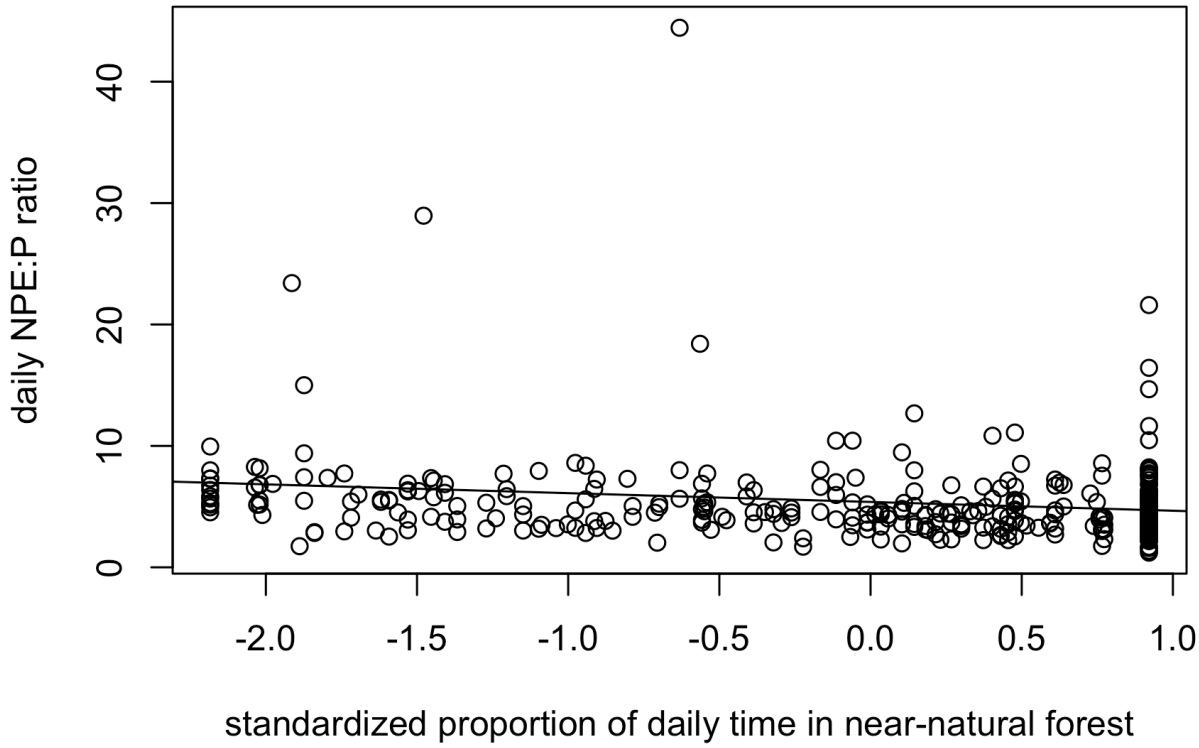


Figure 3.11. Negative relationship between NPE:P ratio and standardized proportion of daily time spent in near-natural forest. Each point represents a daily NPE:P ratio (N=371). Black line based on slope and intercept of linear mixed model.

Table 3.6. Linear mixed model predicting protein intake (N=371 female-days). Subject ID nested in Group were included as random effects. All continuous fixed effects were standardized z-scores. For reproductive demand, "none" was the reference class. * indicates significance ($p<0.05$).

Fixed effect	Estimate	SE	95% CI			df	t-value	p-value
FAI (ripe fruit) *	0.13	0.04	0.03	–	0.15	169.00	3.53	5.37E-04
Rank	-0.04	0.03	-0.10	–	0.01	357.90	-1.58	0.12
FAI (young leaves)	-0.09	0.05	-0.10	–	0.01	18.00	-1.82	0.09
Time in near-natural forest	-0.01	0.04	-0.04	–	0.09	218.20	-0.25	0.80
Fruit in the diet	6.25E-04	0.03	-0.05	–	0.06	359.90	0.02	0.98
Reproductive demand (none)								
early gestation	0.07	0.11	-0.16	–	0.27	359.40	0.60	0.55
late gestation	-0.08	0.12	-0.28	–	0.19	359.90	-0.63	0.53
early lactation	4.21E-04	0.09	-0.17	–	0.20	359.20	0.00	1.00
mid lactation	0.18	0.13	-0.03	–	0.45	359.50	1.43	0.15
late lactation	0.03	0.09	-0.16	–	0.20	358.40	0.30	0.77
Intercept*	4.54	0.11	4.38	–	4.68	3.70	40.22	5.61E-06

Table 3.7. Linear mixed model predicting deviation from nutritional strategy as a function of dominance rank (0-1 scale, 1 highest). * indicates significance ($p<0.05$). R^2 values are pseudo-R^2 [Lefcheck, 2016]. N=371 female days.

Response variable	Fixed effect	Estimate	SE	95% CI		df	t-value	p-value	fixed effects R^2	random effects R^2
Absolute deviation from mean NPE:P ratio	Rank	-0.04	0.47	-0.97	0.92	20.25	-0.08	0.94	1.92E-05	0.02
	Intercept*	1.93	0.35	1.25	2.62	6.64	5.56	1.02E-3		
Absolute deviation from mean protein intake (kcal)	Rank	1.64	5.13	-8.42	11.70	369.00	0.32	0.75	2.75E-04	0
	Intercept*	39.22	3.18	32.99	45.44	369.00	12.35	<2e-16		
Deviation from mean NPE:P ratio	Rank	0.03	0.52	-0.99	1.05	369.00	0.06	0.95	9.02E-06	0
	Intercept	-0.02	0.32	-0.64	0.61	369.00	-0.05	0.96		
Deviation from mean protein intake (kcal)	Rank	-12.58	7.81	-27.88	2.73	369.00	-1.61	0.11	6.96E-03	0
	Intercept	6.39	4.83	-3.07	15.86	369.00	1.32	0.19		
Number of unique food items per day	Rank	-3.60	1.68	-6.91	-0.20	19.76	-2.15	0.04	1.87	4.32
	Intercept	24.24	1.13	22.07	26.42	9.15	21.50	3.84E-09		

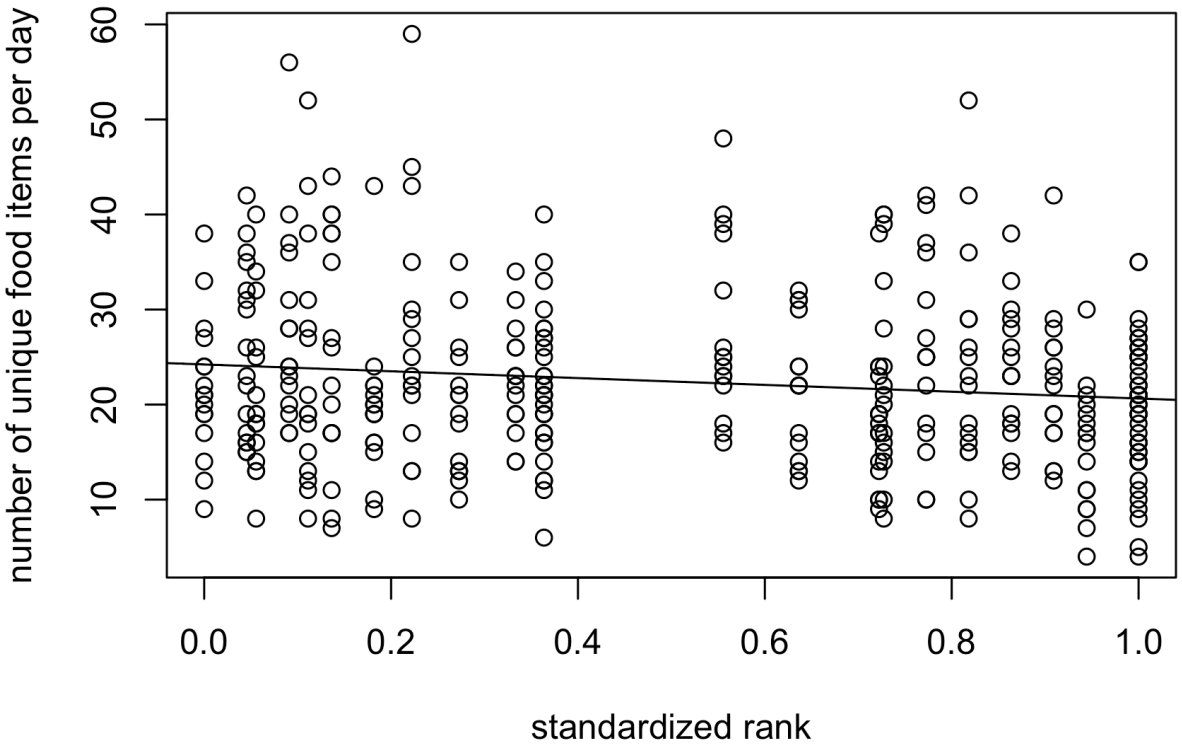


Figure 3.12. Negative relationship between daily unique food items and standardized rank (1=highest). Each point represents a daily follow (N=371). Black line based on slope and intercept of linear mixed model.

Table 3.8. Linear mixed model predicting NPE intake (kcal, N=371 female-days). Subject ID nested in Group were included as random effects. All continuous fixed effects were standardized z-scores. For reproductive demand, "none" was the reference class. * indicates significance ($p<0.05$).

Fixed effect	Estimate	SE	95% CI			df	t-value	p-value
Time in near-natural forest*	-78.28	25.55	-101.62	–	-11.29	176.10	-3.06	2.53E-03
Fruit in the diet*	127.48	20.27	91.03	–	169.50	351.80	6.29	9.43E-10
Rank	-11.16	19.42	-48.59	–	27.03	350.10	-0.57	0.57
FAI (ripe fruit)	24.23	25.75	-45.13	–	42.14	126.00	0.94	0.35
FAI (young leaves)	-35.42	34.34	-70.03	–	9.23	12.00	-1.03	0.32
Reproductive demand (none)								
early gestation	7.87	79.12	-155.46	–	151.52	351.50	0.10	0.92
late gestation	-87.46	86.08	-236.06	–	97.29	351.80	-1.02	0.31
early lactation	-19.06	66.79	-138.23	–	121.06	351.30	-0.29	0.78
mid lactation	40.44	89.44	-121.27	–	224.40	350.80	0.45	0.65
late lactation	1.24	66.11	-132.13	–	125.02	350.60	0.02	0.99
Intercept*	538.46	73.67	425.94	–	644.02	5.20	7.31	6.33E-04

Table 3.9. Linear mixed model predicting total energy intake (kcal, N=371 female-days). Subject ID nested in Group were included as random effects. All continuous fixed effects were standardized z-scores. For reproductive demand, "none" was the reference class. * indicates significance ($p<0.05$).

Fixed effect	Estimate	SE	95% CI			df	t-value	p-value
Time in near-natural forest*	-79.27	27.90	-102.78	–	-4.40	194.80	-2.84	4.97E-03
Fruit in the diet*	126.55	22.06	86.95	–	172.41	361.60	5.74	2.05E-08
Rank	-15.55	21.14	-56.31	–	26.04	359.90	-0.74	0.46
FAI (ripe fruit)	39.71	28.15	-37.92	–	57.13	143.60	1.41	0.16
FAI (young leaves)	-41.98	38.00	-76.85	–	9.48	14.20	-1.11	0.29
Reproductive demand (none)								
early gestation	9.76	86.12	-168.57	–	165.77	361.30	0.11	0.91
late gestation	-95.70	93.71	-255.88	–	107.19	361.60	-1.02	0.31
early lactation	-22.04	72.70	-150.95	–	131.46	361.10	-0.30	0.76
mid lactation	52.75	97.38	-121.61	–	254.88	360.70	0.54	0.59
late lactation	5.28	71.96	-140.22	–	139.85	360.30	0.07	0.94
Intercept*	645.74	82.37	522.73	–	760.24	4.80	7.84	6.37E-04

CHAPTER 4: THE ROLE OF NON-NATURAL FOODS IN THE NUTRITIONAL STRATEGIES OF ADULT FEMALE BLUE MONKEYS IN A HUMAN-MODIFIED MOSAIC LANDSCAPE

INTRODUCTION

An unprecedented amount and rate of human modification of the Earth's land surface characterizes the current Anthropocene [Crutzen, 2006; Steffen et al., 2009]. As a result of human activity, ecosystems increasingly and significantly differ from historical states (and historical ranges of variation); in fact, many seem to be turning into new ecosystems, marked by human-mediated assemblages of species [Hobbs et al., 2009, 2014a]. Whether these ecosystems are irreversibly transforming into novel states, and whether they have intrinsic value, is a subject of debate [Aronson et al., 2014; Hobbs et al., 2014a; b; Murcia et al., 2014]. For example, even though large tracts of intact old-growth forests may uniquely support richness of indigenous taxa [Barlow et al., 2007; Gibson et al., 2011], human-modified forests may offer conservation opportunities [Chazdon, 2003, 2008, 2014; Brockerhoff et al., 2008; Chazdon et al., 2009b]. Many conservationists now call for recognition of the ecological importance of regenerating and regrowing forests [Chazdon, 2014; Hobbs et al., 2014a].

Human-modified habitat is an ecological reality for many species, including those living in the tropics where the majority of forest cover has been altered by human activity [Chazdon, 2014]. Growing human populations in tropical regions create an increasing demand for natural resources, leading to this anthropogenic habitat change [Marsh et al., 2013; Estrada et al., 2017]. Loss and degradation of forest habitat is now the primary threat to the persistence of many tropical mammals [Cuaron, 2000], including nonhuman primates (hereafter primates;

[Estrada et al., 2017]). Many species now occur in mosaic landscapes where patches of natural forest are interspersed with patches of human-modified habitat (i.e. plantations, degraded forest, abandoned farmland, and regenerating secondary forest [Marsh, 2003; Marsh & Chapman, 2013]).

A challenge for researchers is to understand how best to conserve species in these mosaic, human-modified landscapes [Chapman et al., 2016]. The survival of species may be enhanced if fragments of unmodified forest are supplemented with human-modified habitats that retain characteristics useful for a given population's persistence [Chazdon, 2003]. For example, although chimpanzees living in a mosaic of heterogeneous habitat types strongly preferred mature forest habitat for all activity (traveling, resting, foraging, and socializing), they also used coffee plantations for foraging and socializing, and even selected this habitat type over secondary forest [Bryson-Morrison et al., 2017]. Also, lemurs in Madagascar used exotic *Eucalyptus sp*. plantations for resting and traveling, and even fed on the *Eucalyptus* flowers and other plants in the plantation undergrowth [Ganzhorn, 1987]. Similarly, Hending et al. [2018] documented five lemur species resting or foraging in vanilla plantations without eating the vanilla crop, although one species, *Eulemur coronatus*, frequently fed on fruit trees scattered within the plantations. Human-modified habitat may also serve as corridors that reduce the isolation of forest fragments: for example, live fencerows served as connective corridors for five primate species to cross pastures between forest fragments in the Colombian llanos [Carretero-Pinzón, 2013]. In another example, the southern bamboo lemur used habitat fragments dominated by the invasive tree *Melaleuca quinquenervia* as dispersal corridors between more natural littoral forest and swamps and as habitat in which to rest and feed [Eppley et al., 2015]. Finally, increased vegetal complexity of the different habitats in a mosaic landscape may support faunal persistence

because in areas recovering from deforestation, the diversity of recovering plant species is linked to the diversity of recovering animal species [Chazdon, 2015].

If habitat can provide adequate food, negative consequences of human-modification to primates may be mitigated [Fimbel, 1994; Knop, 2004; Irwin et al., 2010; Phoonjampa et al., 2011; Hoffman & O'Riain, 2012; Felton et al., 2013]. Johns & Skorupa [1987] reviewed evidence that many folivores respond positively to forest alteration, perhaps because colonizing vegetation provides ample food. For example, gorilla (*Gorilla gorilla*) density does not decline in response to forest modification, possibly because of the proliferation of herbaceous growth in secondary forests that provides adequate food [Oates, 1996]. For some lemurs, the carrying capacity of their forest habitats increases after low-level modification, possibly because of increased fruit production and protein concentration in leaves [Plumptre & Johns, 2001]. Also, temporal variation in chimpanzee density in two sites (logged and unlogged) in Kibale National Park, Uganda correlated more closely to prevalence of important food items (those composing 75% of diet) than to the historical impact of logging [Potts, 2011]. Even specialist-feeding species, such as Bale monkeys, *Cholorcebus djamdjamensis*, that are thought to be sensitive to habitat modification, may use flexible dietary strategies, such as broadening their diets and focusing less on their primary food (bamboo shoots in this case) as a response to forest fragmentation [Mekonnen et al., 2018].

Some studies of guenons have documented that populations thrive in more altered habitat [Skorupa, 1986; Chapman et al., 2005b]. For example, Plumptre and Reynolds [1994] found a positive relationship between the densities of blue monkeys (*Cercopithecus mitis*) and red-tailed monkeys (*C. ascanius*) and habitat modification (logging) in Budongo Forest, Uganda. Similarly, in Kakamega Forest, Kenya, blue monkey group density correlated positively with higher levels

of modification across four sites [Mammides et al., 2009]. Other studies, however, have found a negative relationship between guenon group density and habitat modification. For example, *C. mitis* and *C. ascanius* group densities were lower in planted forests than natural forests in Kakamega Forest [Fashing et al., 2012]. Similarly, *C. mitis* group density was lower in modified forests, as well as lower in forests with lower plant species richness and diversity, than natural forests in Natal, South Africa [Lawes, 1992]. Finally, *C. mitis* and *C. ascanius* group densities declined after heavy logging in Kibale Forest, Uganda, possibly because food availability decreased when food trees were felled [Chapman et al., 2000]. These variable patterns in guenons may reflect the degree of alteration, and especially the degree to which human-modified habitat offers suitable feeding options, which is hard to compare across studies.

Changes in diet and feeding behavior appear to be the most commonly reported response of primates to human-modified habitat (about 80% of 427 articles [McLennan et al., 2017]). For example, gibbons (*Hylobates lar*), leaf monkeys (*Presbytis melalophos*), and brown spider monkeys (*Ateles hybridus*) responded to habitat modification by shifting their diets to greater percentages of leaves and smaller percentages of fruits [Johns, 1986; de Luna et al., 2017]. Other species increased other components of their diets in response to habitat modification, including mature leaves and lipid-rich fruits (*Eulemur collaris* [Donati et al., 2011]), underground storage organs (*Theropithecus gelada* [Jarvey et al., 2018]), and flowers and petioles (*Alouatta pigra* [Zárate et al., 2014]). One population of blue monkeys (*Cercopithecus mitis)* ate more seeds and shoots [Tesfaye et al., 2013], while another increased consumption of unripe fruit and bark [Fairgrieve & Muhumuza, 2003]. The fact that primates persisting in human-modified habitat often adjust their diets relative to those in more natural habitats suggests that behavioral flexibility, especially dietary flexibility, is key.

An important aspect of dietary flexibility in human-modified habitats may be the incorporation of *non-natural foods*. I expand Brennan et al.'s [1985] and McKinney's [2011] definition of non-natural foods, which included those directly derived from humans or human activity (e.g. via scavenging or crop/food-raiding), to also include exotic (non-native) plant foods, generally introduced inadvertently or for silviculture [USDA; Fischer et al., 2010]. Many studies report non-natural foods in the diets of primates, especially human-derived foods (e.g. *Cebus capucinus* [McKinney, 2011]*, Alouatta guariba clamitans* [Chaves & Bicca-Marques, 2017], *Pan troglodytes verus* [Hockings et al., 2009, 2017; Bryson-Morrison et al., 2016], *Pongo abelii* [Campbell-Smith et al., 2011], *Cercopithecus aethiops* [Cancelliere et al., 2018], *Cebus libidinosus* [Freitas et al., 2008]), but also exotic species (e.g. *Colobus angolensis palliates* [Dunham, 2017], *Colobus vellerosus* [Wong et al., 2006], *Hapalemur griseus* [Grassi, 2006; Martinez, 2008], *Cercopithecus albogularis labiatus* [Wimberger et al., 2017], *Macaca nemestrina* [Ruppert et al., 2018]), or both types (e.g. *Papio ursinus* [Johnson et al., 2013]). Including non-natural foods in the diet may influence activity budgets. For example, groups of South African baboons, *Papio ursinus*, that regularly included more non-natural food in the diet spent less time feeding and reduced traveling [Lewis & O'Riain, 2017]. However, how the inclusion of non-natural foods in the diet relates to foraging effort, quantity or nutritional value of the diet is not yet well known.

Researchers are beginning to document how different types of human-modified habitat (and their associated non-natural foods) influence the nutritional state of consumers ([Birnie-Gauvin et al., 2017]; *Ursus arctos* [Coogan & Raubenheimer, 2016], *Threskiornis moluccus* [Coogan et al., 2017]). To date, however, few such studies have focused on primates. Rode et al. [2006] used scan samples of feeding behavior to study the nutrient and energy intake of six

redtail monkey groups, *Cercopithecus ascanius*, in unlogged and logged forests in Kibale National Park, Uganda and concluded that groups in unlogged forest consumed higher total amounts of lipid and protein. Only one recent study has addressed the value of human-modified habitat from a nutritional ecology perspective, using the Geometric Framework (i.e. assessing if nutrients were consumed in proportion to one another or if critical nutrients were prioritized [Simpson & Raubenheimer, 2012]). Irwin and colleagues [2015] studied five groups of sifakas, *Propithecus diadema*, two inhabiting relatively unmodified habitat and three inhabiting modified and fragmented habitat. Surprisingly, all groups consumed similar diets and balances of nutrients during the "lean" season, when fruit was less abundant. Differences among groups emerged, however, during the abundant season, when groups in modified habitat failed to show an increase in food and nutrient intake, in contrast to those in unmodified habitat. These findings highlight the importance of understanding the link between nutrition and changes in diet related to habitat modification: such changes may have unexpected consequences for the nutritional state of primates.

In this study, I explored the roles of both human-modified habitat and non-natural food in the feeding and nutritional ecology of the blue monkey, *Cercopithecus mitis*. This species has a wide geographic range in African forests, and occurs in various forest types [Lawes et al., 2013]. Blue monkeys sometimes tolerate or respond positively to mild habitat modification [Plumptre & Reynolds, 1994; Mammides et al., 2009]. Overall, though, blue monkey populations appear to persist in human-modified habitats at lower densities when compared to populations in non-modified and unfragmented forests [Skorupa, 1986; Johns & Skorupa, 1987; Thomas, 1991; Lawes, 1992; Chapman et al., 2000; Fashing et al., 2012]. Blue monkeys have the ability to be both largely folivorous and frugivorous, because of a relatively elongated ceaco-colon region and

slow gut passage rates that aid in digestion of a wide range of food types [Bruorton & Perrin, 1988, 1991; Bruorton et al., 1991; Lambert, 1998, 2002]. Their dietary flexibility, the broadest known for guenons [Chapman et al., 2002; Lawes et al., 2013], may explain how they can persist in regenerating secondary and/or human-modified forests that provide both a high diversity of food items and a year-round supply of "maintenance" foods of lower quality (i.e. relatively more difficult to process and digest; [Struhsaker, 1978; Thomas, 1991; Lawes et al., 2013; Tesfaye et al., 2013]). Despite the facts that blue monkeys can live in modified habitats and have highly flexible diets, no study to date has examined how their dietary and nutritional strategies respond to human-modified habitat, nor quantified the value of non-natural foods in their diet.

The Kakamega Forest is an ideal site to study the effects of human-modified habitat on a flexibly feeding primate. This forest supports a stable population of blue monkeys [Fashing & Cords, 2000; Fashing et al., 2012] and includes diverse forest types (ranging from near-natural to abandoned farm/plantation) on a small scale [Mitchell et al., 2009]. The human-modified habitats provide opportunities for monkeys to consume non-natural food. In a village within the study site, monkeys occasionally steal human food refuse. Some surrounding forest areas contain exotic plants, experimentally planted in mono-plantations (e.g. *Bischofia javanica*) or scattered within indigenous forest, that monkeys also consume. In addition, nearby areas of regenerating farmland, overrun with exotic species like guava (*Psidium guajava*), offer other non-natural foods to monkeys. Crop-raiding, a source of non-natural food for other African guenons [Hill, 1997; Baranga et al., 2012; Estrada et al., 2012; Tesfaye et al., 2013], is rare at this site, perhaps because the forest is separated from farmland by a 50 m tea field, which arboreal monkeys avoid. All observed crop-raiding has involved adult males (Cords, pers. comm.) and I did not witness this behavior at all during my study.

I aimed to understand how the dietary habits of female blue monkeys related to non-natural foods, thus supporting population persistence in human-modified habitats and mosaic landscapes in Kakamega Forest. Specifically, I first aimed to describe the prevalence of non-natural foods in blue monkey diets. Second, I asked if habitat use predicted the amount of non-natural food in the diet. I expected that greater use of human-modified habitat would result in more feeding on non-natural foods. Third, I explored the effects of non-natural foods on nutritional strategies. I focused on protein intake and the ratio of non-protein energy (NPE, i.e. carbohydrates + lipids) to available protein (P, hereafter protein) because previous studies of wild primates, as well as my own research [Chap. 2, 3], suggest that many primates prioritize protein intake and balance NPE to P intake [Felton et al., 2009b; Simpson & Raubenheimer, 2012; Johnson et al., 2013, 2017; Irwin et al., 2015; Dröscher et al., 2016; Martínez-Mota et al., 2016]. I expected the dietary flexibility of blue monkeys would allow them to maintain an essentially constant nutrient balance regardless of how much non-natural food they consumed and regardless of the degree to which they used human-modified habitat.

METHODS

Study site: The Kakamega Forest, western Kenya (1650 m elevation, 2000 mm average rainfall) is a semi-deciduous patch (ca. 238 km^2 gazetted in 1933) of a once more continuous Guineo-Congolian rainforest [Kokwaro, 1988; Mitchell, 2004]. The diversity of vascular vegetation is dominated by natural species (96% of recorded taxa [Fischer et al., 2010]). The forest has a long history of human use, described in detail by Mitchell, Schaab and colleagues as part of the Biodiversity Monitoring Transect Analysis in Africa project (BIOTA, www.biota-africa.org; Mitchell, 2004; Lung & Schaab, 2006; Mitchell & Schaab, 2008; Mitchell et al.,

2009). Because of human activity, as well as soil and microclimate heterogeneity, plant communities occur in a mosaic pattern, with varying degrees of modification [Mitchell et al., 2009]. Mitchell et al. [2009] catalogued the communities into four main vegetation classes: *Deinbollia kilimandscharica-Markhamia lutea* alliance, *Celtis mildbraedii-Craibia brownii* alliance, grass- and bush-land, and plantations. All communities reflect some degree of human modification. The most destructive human activity was logging, with concessions granted to saw-millers from the 1930s-80s. Gold miners, active along some streams in the 1930-40s, also had an important effect, introducing guavas (*P. guajava*), a prolific invasive that has spread widely today. Other notable non-natural species are *Solanum madagascariensis*, which is common along roadways and wide paths, and *B. javanica*, which occurs both in large monocultures and scattered singly throughout the forest (experimental plantings).

The study area (centered approximately at 0^{o} 19' N, 34^{o} 52' E) was a ca. 2 km^2 area located along the western edge of the forest, in an area known as Isecheno. For the purposes of data analysis, I simplified BIOTA's vegetation classifications and identified three forest types that were likely biologically relevant to blue monkeys, as they differed in human-use history and current plant composition and diversity (Figure 4.1).

(1) *Near-natural forest* was mainly old (>50 yrs) secondary forest of native plant species, though some non-natural plant species (mainly *B. javanica*) were heterogeneously distributed therein, mostly along trails. Some near-natural forest in the study area was subject in the past both to gold prospecting and logging, though the forest has been largely unmodified by large-scale human activity since the 1980s or earlier [Fashing & Mwangi Gathua, 2004; Fashing et al., 2004; Mitchell, 2004]. Transect data show that near-natural forest was the most vegetation-dense habitat (mean: 60 m^2 basal area/ha, calculated as the sum of means for each species, including all

plants ≥5 cm DBH (diameter at breast height); [Chap 2]). Native plants predominated: the most prevalent exotic species ranked only 29th in terms of basal area (Table 4.1, Chap 2), and only 1% of the cumulative basal area constituted exotic species (Table 4.1, Chap 2). BIOTA classified this habitat as *Celtis mildbraedii-Craibia brownii* alliance as well as mixed plantation [Mitchell et al., 2009].

(2) *Village forest* included the ca. 8 ha grounds of the Kakamega Forest Station, where the Kenya Forest Service had houses, offices, a health clinic, canteen, and tourist accommodations (huts and a bungalow). The ground around these buildings was largely grassy, but the station also included small kitchen gardens and a tree nursery (1.6 ha) with extensive bare soil, where several individual non-natural trees were planted, most notably a large oil palm, *Elaeis sp*. Tree cover outside the nursery was light compared to the near-natural forest, but nonetheless allowed monkeys to move through the village using arboreal routes. The village forest was the least dense in terms of vegetation (mean: 14 m^2/ha; [Chap 2]). None of the measured non-natural plants were cultivated crops. The most prevalent species in the village forest (*B. javanica*) was non-natural, as was the fifth most prevalent species (Table 4.1). Overall, 40% of basal area constituted non-natural plants (Table 4.1; Chap 2). Humans occupied the village forest year-round, with about 30 people living in the ~8 ha village, plus 10-30 additional people as daytime visitors (workers in nursery, tourists).

(3) *Farm/plantation forest* occurred mainly in the southern portion of the study site. The name reflects its land use history: during the 1930s-80s, some of these areas were family farms, or *shambas.* The government reclaimed these farms in the 1980s, and allowed the land to regenerate naturally: at the time of this study, invasive plant species, especially *P. guajava*, had become very common and crop plants were no longer growing. Large, exotic *Eucalyptus saligna*

also grew scattered throughout the area. In addition, many edge specialist trees and shrubs such as native *Harungana madagascariensis* and exotic *S. mauritianum* were common. Farm/plantation forest also comprised larger tracts that had been logged and replanted, mostly in the 1940s, with exotic mono-cultures of *Pinus patula*, *B. javanica, Grevillea robusta,* and *Cupressus lusitanica*. At the time of this study, these planted areas were not actively managed. Transect data showed that farm/plantation forest had almost the same basal area as the near-natural forest (mean: 61 m^2 basal area/ha; [Chap 2]). However, non-natural plant species dominated this vegetation type, with the five topmost species being non-natural and overall, 88% of basal area representing non-natural plants (Table 4.1; [Chap 2]), none of which were cultivated crops. I refer to the village forest and farm/plantation forest collectively as human-modified habitat.

Study subjects: The study area supported a dense population of blue monkeys [Fashing et al., 2012], which have been studied since 1979 [Cords, 2012]. Subjects came from 3 habituated groups (8 per group), and were distinguishable based on natural features. All subjects were parous and in various reproductive states (births occur seasonally, every 2-3 years per individual; Cords & Chowdhury, 2010). Subjects within each group also varied in rank, with four subjects of relatively high rank and four subjects of relatively low rank in each group.

Each group's home range (GN: 23.9 ha, GSC: 41.8 ha, TWS: 52.3 ha) included 2-3 habitat types, with differing proportions (Figure 4.1, [Chap 2]). GN's range was mostly near-natural forest (92%) but also included a portion of the village forest [Chap 2]. GSC had the second largest home range, of which 44% was farm/plantation [Chap 2]. TWS had access to all three habitats: their home range comprised 85% near-natural forest, 2% farm/planation forest (though they did not feed in this forest type), and 13% village forest [Chap 2]. Since Cords

started monitoring this study population, the population has grown in size via natural reproduction (about 55 individuals in 1995 to 250 individuals in 2012), but maintained its density by expanding into adjacent areas [Cords, 2012, unpub; Fashing et al., 2012]. Blue monkeys began to use the village forest in 1997 [Cords, 2012]. They also recently (ca. 2008) began to use the farm/plantation forest for extended periods. Comparison of groups with vs. without access to the forest station, as well as before and after TWS began using the village, revealed that life history parameters did not change [Cords, 2012]. Thus overall it seemed that the monkeys' use of the village and farm/plantation forests was a relatively new behavior that has not limited population persistence. Further, individual daily path length, a proxy for energy expenditure, did not significantly relate to daily caloric intake [Chap 2], suggesting that females were not energetically limited. Finally, since in fact the population has grown over the last two decades, I assumed in this research that females in all three groups were able to access adequate food resources to maintain their weight and avoid substantial energy or nutrient deficits over the long term.

Anthropogenic influence on study population: To facilitate future meta-analysis, I classified the degree of anthropogenic influence on the study population using McKinney's [2015] framework. I used the proposed four-letter system to describe the following features: landscape, diet, human-nonhuman primate interface, and predation. Kakamega blue monkeys should be categorized as DDKG. Landscape was classified as D (minor levels of current or recent habitat modification, habitats divided by roads or small-scale resources extraction), diet was classified as D (mostly wild foraged, with opportunistic theft or provisioning of human foods), human-nonhuman primate interface was K (researchers plus others, primarily local people, with minor interactions, such as photographing animals or anthropogenic noise), and

predation was G (human predation present (often with dogs as helpers), with subsistence hunting by humans, plus reduced pressure from indigenous predators).

Data collection

Data collection methods for nutritional ecology studies of primates comprise two main parts: 1) field work to sample behavior, monkey feces and food items, and 2) laboratory work to analyze physical samples for nutrient composition. I followed methods established by Rothman and colleagues [2012, 2013].

Feeding observations: A team of trained observers [Chap 2] sampled each subject approximately twice a month between January and September 2015 (N=15-16 samples per female for a total of 371 female-days), spacing repeated samples of each individual at intervals of >1 week (mean 15.4 ± SD 5.9 days, N=347 intervals). The team conducted all-day focal follows [Altmann, 1974; Chap 2], the most accurate method to document daily diet [Felton et al., 2009a; Rothman et al., 2012, 2013]. Subjects were in sight for a mean 9.1 ± SD 0.2 hr and out of sight for 0.7 ± 0.2 hr (not including time in the morning spent searching for group and focal subject). In each focal follow, the team and I measured the quantity of consumed food by counting ingested units, defined as an observably consistent amount of food that was species-specific (e.g. a single *Mimulopsis solmsii* leaf, a 1 inch section of *B. javanica* stem).

Identification of non-natural foods: In Kakamega, non-natural foods of blue monkeys included 1) exotic plants that were introduced either inadvertently or for silviculture and 2) human-derived foods (usually refuse, including scraps of cultivated foods (e.g. banana peels discarded by tourists). Study subjects did not engage in crop-raiding. In Fischer et al.'s [2010] annotated list of 986 Kakamega Forest vascular plants, 36 were categorized as exotic (17 of which blue monkeys apparently did not eat). Most exotic plants were naturalized and some were

invasive. Two species eaten by monkeys (*Brunfelsia pauciflora*, *Elaeis* sp.), both planted in the village forest, were not included in Fischer et al. [2010], so I used local floras [Blundell, 1982; Beentje, 1994] and consulted local experts to confirm that they were exotic.

Habitat use: To track habitat use, the team recorded GPS coordinates (every 30 min, on the hour and half hour) of focal subjects using handheld Garmin GPSMAP® 60 CSx devices with an error of ±5 m or less [Chap 2]. The team did not record a GPS point when the focal animal was out of sight in an unknown location. The GPS records allowed me to specify the percentage of a day (i.e. percentage of daily GPS records) each subject spent in the three habitat types, once I had combined them with GIS maps of the habitat boundaries [Chap 2].

Food sample collection: I collected samples of plant foods and whenever possible, from individual plants that monkeys used for feeding [Rothman et al., 2013; Chap 2]. I collected most insects opportunistically, as observed insect predation events were quick and precluded collection. Social insects (like ants) were collected, if possible, at time of feeding observation [Chap 2].

I organized food samples by species-specific food parts collected on a particular day. For each sample, I recorded weights of 50 units (i.e. the observably consistent amounts recorded during focal follows) of fresh sample, not more than 6-12 hours after collection in the field and then calculated a mean unit weight [Chap 2]. Before weighing, I processed the food items in a way that matched what I observed the monkeys doing (e.g. peeling the stem; [Rothman et al., 2013]).

I dried food samples primarily during the day at 55 ° C in a solar-powered dehydrator (custom designed by Bruce Cameron of Nango Solar Limited, Kisumu) and during the dry season, in a warm dark shed [Chap 2]. Samples typically dried over the course of a few days

(range: 1 day to 1 week). I kept samples from sun exposure and discarded any that were moldy [Rothman et al., 2012; Chap 2].

Fecal sample collection: The team collected a fecal sample from a given female one day after each focal follow. If it was not possible to obtain a sample from the previous day's focal follow, we tried to collect a sample from another adult female from the group. We placed approximately 5-10 ml fresh sample in sterile Corning 15 ml plastic sample tube, pouring in enough ethanol to cover the sample, and sterilized it for at least three days [Rothman et al., 2012]. I dried samples in the tubes in an oven at 55 ° C at the Kenya Agricultural & Livestock Research Organization in Kakamega town. I then sealed the tubes with Parafilm for future analysis to assess digestibility of fiber (see *Nutritional analyses* below).

Nutritional analyses of samples: I conducted all lab work in the Rothman Nutrition Lab, Hunter College, City University of New York. Using wet chemistry techniques, I measured the percentage composition of the following nutritional parameters in monkey foods [AOAC, 1990; Rothman et al., 2012]: structural carbohydrates (cellulose, hemi- cellulose, lignin, measured via neutral and acid detergent fiber (NDF and ADF) and acid detergent lignin analyses (ADL)), available protein (subtracting acid detergent insoluble protein from crude protein amount from combustion), ash (i.e. minerals, measured through combustion and correcting for fiber bound ash), and crude lipid (via ether extraction; [AOAC, 1990; Licitra et al., 1996; Palmquist & Jenkins, 2003; Conklin-Brittain et al., 2006; Rothman et al., 2012]). All measurements were on a dry matter basis. I computed percentage of non-structural carbohydrates by subtracting from one the sum of NDF (i.e. structural carbohydrate estimate), available protein (hereafter protein), lipid, and ash [Rothman et al., 2012].

An animal's gut physiology determines its ability to digest fiber via microbial fermentation. To determine the energetic gain from fiber, I used the amount of lignin in the fecal sample as a physiological marker for fiber fermentation. I compared the lignin contents in the daily diet to the corresponding fecal sample to calculate fiber digestibility coefficients that represent the fraction of the ingested fiber that was fermented and subsequently digested [Fahey & Jung, 1983; Van Soest, 1994; Rothman et al., 2012]. Captive blue monkey females had a mean gut retention time of plastic markers of 20.6 (± 12.8 SD) hours [Lambert, 2002], so I related a daily diet from a focal follow day to the fecal sample collected the following day. I calculated fiber digestibility coefficients as defined in Conklin-Brittain et al. [2006] and Rothman et al. [2008b].

Near infrared reflectance spectroscopy (NIRS) analysis: In addition to wet chemistry, I used NIRS to analyze plant foods [Rothman et al., 2012; Chap 2]. When irradiated with near-infrared light, a sample reflects a unique vibrational energy spectrum based on chemical bonds. These spectra are then matched and calibrated against their reference values from traditional wet chemistry analysis. Calibrated spectra are grouped according to plant parts to create predictive equations, which allow estimation of the nutritional values for samples of the same plant part. This technique has been shown to measure accurately the nutritional content of primate diets [Rothman et al., 2009, 2012].

Additional nutritional values: The dataset included ten human-derived foods: chicken egg, maize, *ugali* (cooked maize flour), banana, mango, orange, sweet potato, cabbage, watermelon and sugarcane. I analyzed maize and *ugali* samples in the lab and obtained nutritional parameters of the other eight from the USDA website (https://ndb.nal.usda.gov/ndb/).

Nutritional values of insects were determined using wet chemistry lab techniques by P. Wakaba at the Kenya Agricultural & Livestock Research Organization, Muguga campus.

Daily diet intakes: I calculated daily intake of macronutrients (hereafter nutrients) per focal follow by multiplying the observed quantity of food consumed (number of units x unit weight) by the food's nutritional value (percentage composition of a given macronutrient, e.g. % protein per unit weight), then summing these values across all foods consumed. I reported the following measures (in g, dry matter basis): TNC, lipid, protein, NDF, ADF, ADL, ash, and total food (sum of TNC, lipid, protein, NDF, and ash). I then converted nutrient intakes (in grams) to energetic values (kcal) using the following conversions: 4 kcal/g for non-structural carbohydrate, 4 kcal/gram for protein, 9 kcal/g for lipid and 3 kcal/g for fiber [Conklin-Brittain et al., 2006]. The caloric value of fiber was adjusted by multiplication with a fiber digestibility coefficient specific to each group [Conklin-Brittain et al., 2006; Chap 2]. I reported the following measures (in kcal): TNC, lipid, protein, NDF, and total energy (sum of TNC, lipid, protein, and NDF).

Data analysis

I ran all statistical models and graphics in R, version 3.3.2 [R Core Team, 2016]. I used the following statistical packages: MASS [Venables & Ripley, 2002], lme4 [Bates et al., 2015], lmerTest [Kuznetsov et al., 2016], GAMLSS [Rigby & Stasinopoulos, 2005], ggplot2 [Wickham, 2009], popbio [Stubben & Milligan, 2007] and piecewiseSEM [Lefcheck, 2016]. I validated all models by checking the residual distribution, plotting residuals against predictors and plotting a Q-Q plot [Zuur et al., 2009; Ieno & Zuur, 2015]. For any model with multiple predictors, I verified that they were not collinear by examining Pearson correlation coefficients using a cut-off of 0.8 [Zuur et al., 2009; Ieno & Zuur, 2015].

Habitat use: I calculated habitat use using the GPS points from focal follows [Chap 2]. To investigate habitat preference, I compared daily observed habitat use with habitat representation in the home range.

Relationship between time spent in human-modified habitat and non-natural food in diet: To analyze how time spent in human-modified habitat was related to the proportion of the daily diet comprising non-natural foods, I used a zero-inflated beta regression [Ferrari & Cribari-Neto, 2004; Rigby & Stasinopoulos, 2005; Smithson & Verkuilen, 2006; Ospina & Ferrari, 2010, 2012]. Beta regression is particularly suited for this type of analysis because it can model the data when the dependent variable is continuous (proportion of diet comprising non-natural foods), highly skewed (in this case, positively), and/or inclusively bounded by 0 and 1. One assumption of the model is that the biological process(es) that generated 0s in the data are fundamentally different from the process that generated continuous values between zero and one [Zuur & Ieno, 2016]. This situation could reasonably apply to the data here as 0s may be generated when groups did not have access to a habitat type on a given day (e.g. from losing an intergroup encounter), while values between zero and one may be generated by a group's choice to preferentially move into a habitat type and consume non-natural foods. The data did not contain any values of one for the dependent variable (i.e. an entire daily diet sourced from non-natural foods). For these models, I used the package "GAMLSS" with the distribution family "BEZI" (BEta regression with Zero Inflation) in R [Rigby & Stasinopoulos, 2005; Stasinopoulos et al., 2008].

In zero-inflated beta regressions, the data are fit using at least two formulas. The first (i.e. mu) uses a beta distribution for the continuous data bounded by 0 and 1 and a logit link function. The second formula (i.e. nu) first converts values >0 to 1s and then uses a Bernoulli distribution

for the 0s and "1s" with a logit link function [Stasinopoulos et al., 2008; Zuur & Ieno, 2016]. To model the proportion of calories from non-natural foods in a female's daily diet, I used proportion of the day that was spent in human-modified habitat (the village forest and farm/plantation forest) as a fixed effect and included Subject and Group ID as random effects. I used a likelihood ratio test with maximum likelihood (LRT; all LRTs mentioned henceforth also used maximum likelihood) to compare the full model to one with only random effects.

To evaluate group differences in nutrient and energy intake of non-natural foods, I ran linear mixed models with restricted maximum likelihood and a Gaussian distribution [Bates et al., 2015; Kuznetsov et al., 2016]. I used one model for each of 7 dietary constituents of the daily intake that came from non-natural food: total energy (kcal), TNC (kcal), lipid (kcal), NDF (kcal) and protein (kcal), food intake (g, DW basis), and NDF (g, DW basis). In all models, group was the fixed effect and Subject ID was a random effect. Also for all models, I used a likelihood ratio test to compare the full model to one with only random effects.

Impact of non-natural foods on nutritional ecology: I distinguished non-natural (N=112) vs. natural feeding days (N=259) according to the type of food that provided > 50% of daily calories. I built two linear mixed models with restricted maximum likelihood and a Gaussian distribution, one with the ratio of NPE:P and one with the amount of protein (in kcal) as the response variable. Both models used type of feeding day as a fixed effect and Subject ID nested in Group as random effects. For both models I used a likelihood ratio test to compare the full model to one with only random effects.

I used the Geometric Framework (GF) to visualize the impact of non-natural foods on the nutritional strategy, combining the nutritional measures derived from lab analysis with behavioral data on diet selection [Simpson & Raubenheimer, 2012]. In the GF, axes represent

nutrients, and I plotted daily nutrient intakes as Cartesian points (showing amounts of nutrients, in kcal, in the daily diet). OLS regressions indicated how tightly intake was regulated among non-natural feeding days versus natural feeding days (by comparing R^2 values and coefficients of variation; [Simpson & Raubenheimer, 1995]).

Nutritional space of non-natural versus natural foods: To visualize the nutritional space of the diet of blue monkeys, I used a Right-angled Mixture Triangle (RMT; [Raubenheimer, 2011; Raubenheimer et al., 2015]). This geometric representation is a variant of the more established ternary plot (also called a de Finetti diagram or triangle plot). The advantage of an RMT plot is that it is right-angled and reading values of points is more intuitive than equilateral triangle plots. The RMT is based on a Cartesian plane, with the implicit third axis a series of negative-sloped isoclines from 0% to 100%. The values of a particular point on the plot must sum to a constant, K. Thus, it is easy for one to see the x and y values of a point and then deduce the implicit value of the third axis by K-x-y. For RMT in nutritional geometry, it is particularly well suited for plotting since there are three macronutrients that contribute to energy intake: lipid, protein, and carbohydrate. A nutritional space is defined by a set of points bounded by a minimum convex polygon. An organism can arrive at any diet contained within the polygon by consuming a mixture of the different foods composing the polygon.

RESULTS

Non-natural foods: Over the study period, subjects fed from 15 exotic plants species and 10 human-derived foods (Table 4.2), for a total of 47 species-specific non-natural food items. Only one food item, a chicken egg, represented non-natural animal matter food. Overall, females put most foraging effort (>1% of total feeding time) into five species of non-natural plants: *B.*

javanica, P. guajava, C. lusitanica, S. mauritianum, and *Lantana camara* (Table 4.2). Together, these five species accounted for 95% of time feeding on non-natural foods. An average female consumed a third (range 15-71%, N=24 females) of her daily calories from non-natural food resources (Table 4.3). Females derived most non-natural calories from TNC, followed by lipid, NDF, and protein.

Group-wide comparison allows an assessment of how access to human-modified landscapes affects the inclusion of non-natural foods in the daily diet. Females in different groups differed in terms of how much non-natural foods contributed to energy intake, and which particular species of non-natural foods they consumed, as well as their relative importance. Not surprisingly, females in GSC (the group whose home range had most human-modified habitat) consumed significantly more nutrients and energy from non-natural foods than females in the other two groups (Table 4.4, Figure 4.2, Table 4.5). Specifically, they consumed higher daily caloric amounts of protein, TNC, total energy, NPE and NDF and more daily grams of NDF, ADF, ADL and total food from non-natural sources. The only nutrient for which the pattern did not hold was lipid; females in GSC and TWS groups ate more lipid (kcal) from non-natural foods than females in GN, but intake did not differ between the first two groups.

Like the pattern of absolute intake, the percentage of calories sourced from non-natural foods was highest for GSC (55%), and lowest for the two other groups (GN: 22% and TWS: 25%; Table 4.3). For important foods (those composing >1% of all calories consumed by females in a group), groups differed both in how many were non-natural and which non-natural foods they consumed (Table 4.6). GN had a diet with two important non-natural food items and GSC's diet included three, while TWS had twice that number (six important non-natural foods). *B. javanica* fruit and *S. mauritanium* fruit were important to all groups, and *B. javanica* fruit was

among the top three food items in each (Table 4.6). *P. guajava* fruit was important to GSC and TWS. Two food items, *Elaeis sp*. fruit (oil palm) and *ugali* (cooked maize flour), were important only to TWS. While all important foods (natural and non-natural) together represented a similar percentage of calories in diet for each group (72% for GN, 73% for TWS, and 74% for GSC), the groups differed in the proportion of calories of important foods comprising non-natural foods (26% for GN, 34% for TWS, and 77% for GSC, (Table 4.6; [Chap. 2]).

Habitat use by type and group: Females in different groups spent different percentages of their day in human-modified habitats (GSC: 60%, TWS: 23%, GN: 7%, Table 4.7). Moreover, females in two groups used human-modified habitat disproportionally (Table 4.6). Specifically, females in TWS used village forest twice as much as expected from the habitat's representation in the home range. Females in GSC used farm/plantation forest a third more than expected from the habitat's representation in the home range. In contrast, females in GN appeared to use human-modified habitat in proportion to its representation.

Relationship between time spent in human-modified habitat and percentage of non-natural food in the diet: A quarter of the data represented days when females did not spend any time in human-modified habitats, but still ate non-natural foods (N=87 days). Of those days, females ate a mean 26% of their calories from non-natural foods (SD=23%, range=<1-92%, N=87 female-days). Non-natural food plant species were scattered throughout the secondary forest, and blue monkeys exploited them as food resources there: in fact there were 13 female-days when subjects consumed >50% of the diet from non-natural food resources, but spent no time in human-modified landscapes. On days when subjects spent time in human-modified habitat, they consumed a mean of 43% of their calories from non-natural foods (SD=29%, range=0-97%, N=284 female-days).

Time in human-modified habitat significantly predicted the proportion of daily caloric intake from non-natural foods (LRT: X^2 (df=2.89)=126.80, p <0.01). Both the mu and nu portion of the model indicated a positive and significant relationship between time in human-modified habitat and the probability of eating non-natural foods as well as the proportion of calories from such foods (Table 4.8, Figure 4.4).

Nutrient balancing for natural feeding versus non-natural feeding days: On non-natural feeding days, females ate significantly higher NPE:P ratios than on natural feeding days (Table 4.9, Figure 4.4, LRT comparing full model vs. random effects only, X^2 (df=1)=58.90, p=1.67-14). On average, females ate approximately two thirds more NPE per unit of P on non-natural feeding days than on natural feeding days (non-natural day NPE:P mean ratio=7.2 ± SD 5.3, N=112 female-days versus natural feeding days NPE:P mean ratio=4.3 ± SD 1.8, N=259 female-days, (Figure 4.4)). In addition, on natural feeding days, females adhered more tightly to a NPE:P balance (CV=41%) than non-natural feeding days (CV=74%). The eight most extreme NPE:P ratios (range: 14.7-44.4) occurred on non-natural feeding days by females in TWS and GN group. In contrast, on non-natural feeding days, females did not eat significantly different amounts of protein (kcal) than on natural feeding days (Table 4.9, Figure 4.5, LRT: X^2 (df=1)=0.94, p=0.33). Also, protein intake fluctuated to a similar degree on non-natural and natural feeding days (CV=46% on non-natural feeding days vs. 51% on natural feeding days).

Nutritional space of non-natural foods compared to that of natural foods: A RMT plot showed that the nutritional space of non-natural foods encompassed 66% of the nutritional space of natural foods (Figure 4.6). Further, the majority of non-natural food items occupied similar nutritional space as their natural food item type counterparts (e.g. non-natural stems and natural stems were similarly positioned). An exception was oil palm fruit (*Elaeis sp*.), which extended

the nutritional space of non-natural foods: without the oil palm fruit, the nutritional space of non-natural foods would be almost entirely encompassed (99%) by the nutritional space of natural foods. Not surprisingly, the point representing a chicken egg, a non-natural food item, was similarly located to the points representing insect morphotypes, showing characteristic high lipid and protein values. The point for sugarcane clustered near the points representing exudates, in the nutritional space of high carbohydrates and low lipid and protein. The points for the other human-derived foods occurred in the nutritional space occupied by many other food items that were low in lipid content and variable in protein and carbohydrate content.

DISCUSSION

Female blue monkeys at Kakamega incorporated a substantial amount of non-natural food in their diets. Overall, they focused the majority of feeding time on only five species of non-natural plants and ate approximately a third of their daily calories from non-natural foods. Females derived most non-natural calories from TNC and least from protein.

Females in different groups varied in relative use of non-natural food items. Females in the group with the most human-modified habitat in its range (GSC) used non-natural foods the most extensively, consuming higher daily amounts of nutrients and energy (including more than half their calories) from them. Females in one other group (TWS) also ate high amounts of lipids from a non-natural source, namely the high-fat fruits of a single, exotic oil palm (*Elaeis sp.)*.

Females in two of the three groups preferred human-modified habitats (farm/plantation forest and village forest, respectively), while females in GN group used different habitat types in proportion to their abundance. Not all human-modified habitat was preferred, however, as GN did have access to such habitat but showed no preference, and TWS actually avoided a stand of

Pinus patula in their home range, using it only to travel but not to feed. Preference for human-modified habitat largely matched its availability in each group's home range: GSC's range included the largest area of farm/plantation forest and they showed a clear preference for it. TWS's range included a larger area of village forest than GN's, which preferred this habitat less.

The use of human-modified habitat positively predicted inclusion of non-natural food in the diet. When females spent any time in human-modified habitat, they consumed a mean 43% of their calories from non-natural foods. Even when females did not use human-modified habitats, they still derived a mean 26% of their calories from non-natural foods. The majority of non-natural foods provided similar access to nutritional space as natural foods. The most notable exception came from oil palm, *Elaeis sp.*, fruit, which was higher in fat compared to all other food items (Appendix I).

The inclusion of non-natural foods in the diet drove variation in the nutritional strategy. Females maintained a higher NPE:P ratio when they consumed a daily diet with more than half the calories derived from non-natural foods, as compared to daily diets on other days. They also showed more variation in NPE:P on non-natural vs. natural feeding days. In contrast to observed variation in the NPE:P ratio, protein (kcal) intake did not differ on days when females did or did not feed on a majority of non-natural foods. This consistency of protein intake agreed with findings from Chapters 2 and 3, which documented how daily protein intake varied little throughout the study and between periods of high and low fruit availability. Prioritization of protein, coupled with the fact that females had higher NPE:P ratios when feeding mostly on non-natural foods, indicates that blue monkeys capitalized on non-natural resources to maximize NPE intake as long as they were able to regulate protein intake [Simpson & Raubenheimer, 2012]. What remains unclear though, is whether there are adaptive advantages associated with the

ability to consume diets of variable NPE:P ratios when primates are presented with nutritionally dense non-natural foods.

It seemed that blue monkeys responded to human-modified habitat (and the non-natural foods it offered) in a similar fashion to how they, and other primates, respond to seasonality of food resources. Namely, primates adjust to different foraging conditions by tolerating a range of NPE:P values and also adjusting NPE:P ratios while still prioritizing critical nutrients. Blue monkeys ate diets with higher NPE:P ratios when the percentage of fruit in the diet was higher, but still prioritized protein, whose intake did not change in response to the amount of fruit in the diet [Chap 3]. Both blue monkeys and spider monkeys, *Ateles chamek*, tolerated a similarly wide range of NPE:P ratios [Felton et al., 2009b]. Blue monkeys consumed daily diets with NPE:P ratios ranging from 1.2:1 to 44.4:1 with an average of 5.2:1 [Chap 3]. For spider monkeys, Felton et al. [2009b] reported a range of daily NPE values (0.7-6.2 MJ/day, mean=1.82 MJ/day) and a consistent mean P intake (0.19 MJ/day), from which one can calculate a conservative range of NPE:P ratios of 4:1 to 33:1, with a mean value of 9.5:1 (daily diet data from 18 individuals over the course of 9 months [Felton et al., 2009b]). These two populations show the largest ranges of daily NPE:P ratios reported to date. In addition to tolerating wide ranges of NPE:P values, both species prioritized protein intake by eating consistent amounts throughout study periods of 8-9 months [Felton et al., 2009b]. NPE intake, by contrast, varied as a function of ripe fruit availability for both species, and also as a function of the inclusion of non-natural foods for blue monkeys [Felton et al., 2009b; Chap 3]. Similarly, black howler monkeys, *Alouatta pigra*, responded to the *nortes* season (characterized by cooler temperatures) by reducing amount of fruit in diet and reducing NPE intake; however, monkeys kept protein intake constant across the dry, wet, and *nortes* seasons [Martínez-Mota et al., 2016]. White-footed sportive lemurs,

Lepilemur leucopus, also appeared to maintain protein intake across seasons, but varied NPE intake from the wet hot to dry cold seasons [Dröscher et al., 2016]. Protein prioritization may be a common way for primates to respond to seasonal or spatial changes in food availability.

In contrast to the above examples of protein prioritization, gorillas (*Gorilla berengei*) prioritized NPE intake across seasons and allowed protein intake to vary, resulting in higher mean NPE:P ratio during the fruit-eating season (3:1) than during the leaf-eating season (2:1; Rothman et al., 2011]). Gorillas also ate diets that varied in NPE:P ratio, though considerably less than those of blue monkeys or spider monkeys (range: 0.3:1 to 17:1 over the course of 319 days; [Rothman et al., 2011]). There are examples, though, of primates responding differently than the above examples to seasonal changes in foods, perhaps because of the intense seasonality in Madagascar (similar NPE:P ratios, but lower nutrient intake overall from abundant to lean season in diademed sifakas, *Propithecus diadema* [Irwin et al., 2015], and reduced nutrient and energy intake from wet to dry season in Verreaux's sifakas, *Propithecus verreauxi* [Koch et al., 2017]). Javan slow lorises, *Nycticebus javanicus,* possibly prioritized fat between wet and dry season in [Cabana et al., 2017].

As habitat becomes more fragmented and modified, researchers are beginning to document the degree of inclusion of non-natural foods in the diets of primates, including their nutritional contribution. This study has shown that non-natural foods can be very important: for blue monkeys at Kakamega, they contributed from one fifth to more than a half of the calories in the diet. Similarly, a study on the nutritional ecology of a single female chacma baboon found that both human-derived foods and non-natural food plants were regularly included in the diet, with two notable species of non-natural food items, nuts from *Pinus pinea* and acorns from

Quercus sp. contributing 44% of energetic intake over the course of 30 days [Johnson et al., 2013].

While not reporting from a nutritional or energetic perspective, some studies have documented the fact that primates regularly and extensively incorporated non-natural foods into their diets. For example, blue monkeys living in fragmented forest in Ethiopia crop-raided seeds from barley and wheat, deriving 33–41% of their diet (based on time spent feeding) during 2 of 10 study months [Tesfaye et al., 2013]. Two groups of samango monkey, *Cercopithecus albogularis (mitis) labiatus*, concentrated more than half of their annual diet on the non-natural black wattle, *Acacia mearnsii* [Wimberger et al., 2017]. Bamboo lemurs, *Hapalemur meridionalis*, fed on two non-natural plants in 33 out of 36 study months while the collared brown lemur, *Eulemur collaris*, fed on 3 species of non-natural plants for 4 of 19 study months [Eppley et al., 2017] and vervet monkeys, *Chlorocebus pygerythrus*, fed on 25 non-natural and crop plants during three years of observation in Uganda [Chapman et al., 2016]. Three groups of guerezas, *Colobus guereza*, in Entebbe Botanical Gardens, Uganda relied on 81 food plant species, of which 26% were non-natural and one group spent 37% of feeding observations on one non-natural species of rubber tree [Grimes, 2000]. One group of colobus, *Colobus vellerosus*, living in a forest fragment in Ghana, ate a diet that included a non-natural plant as their fourth most frequently eaten species [Wong et al., 2006].

Evidence also exists that primates may use non-natural food resources regardless of degree of habitat modification. For example, over the course of 18 months and 267 full-day follows, Dunham [2017] studied the diets of 3 groups of Angolan colobus monkeys, *Colobus angolensis palliatus,* that lived in habitats that ranged in degree of modification. Dunham observed that groups inhabiting more modified habitat did not rely more on non-natural foods

than the group in less modified habitat. Instead, all three groups derived 30-40% of total diet (based upon feeding time) from 10-13 non-natural species, 2-5 of which were in each of the group's top 20 species eaten.

Additionally, primates may seasonally rely on non-natural foods when natural food resources are scarce. For example, Bicca-Marques and Calegaro-Marques [1994] found that non-natural food items and specifically the fruit of the orange tree, *Citrus sinensis*, served as staple foods (accounting for >20% of feeding records/month) when natural fruits were seasonally not available to one group of black howler monkeys in a semi-natural forest fragment in Brazil. Approximately 40% of food plant species and 38% of feeding records included non-natural species and in five of the twelve study months, *C. sinensis* accounted for >60% of the fruit in the diet (with a peak of 97%, [Bicca-Marques & Calegaro-Marques, 1994]). Similarly, samango monkeys, *C. albogularis (mitis) labiatus,* living in a matrix including residential gardens and plantations in South Africa, fed on non-natural foods inversely to natural food availability [Wimberger et al., 2017]. Non-natural foods, particularly black wattle, *Acacia mearnsi*, and oak acorns, *Quercus robur* and *Q. palustris*, dominated the monkeys' diets on some days (>50-95% of feeding budget). Overall, primates appear to have a high capacity to incorporate non-natural food into their diets.

Moreover, blue monkey females seem to actively seek non-natural foods. Females used human-modified habitats for foraging, a relatively recent result of home range expansion by study groups in 1997 into the forest village and in ca. 2008 into the farm/plantation forest. The range expansion was testament to the dietary flexibility of the species, allowing it to exploit readily available foods, many of them non-natural and a result of human activity (e.g. proliferating invasive and edge species such as *P. guajava*, *L. camara* and *Rubus rigidus)*. In

addition, females in two of the three study groups used human-modified habitats more often than expected by chance and more than females in the third group. Human-modified habitats contained more non-natural food resources than near-natural forest habitat in Kakamega Forest and the attractiveness of these species may explain the high selection ratios. For example, the representation of *B. javanica* (by mean basal area/ha) was 450 times higher in farm/plantation forest and 10 times higher in village forest than in near-natural forest. Similarly, the presence of *P. guajava* was 35 times higher in the farm/plantation forest than in the near-natural forest. Monkeys had access to oil palm from only a single tree in the village forest. Oil palm fruit may have been sought because it represented a high-efficiency food source, providing 5% of all calories consumed by females in the study, but only 0.2% of all feeding time [Chap 2]. Other primates also readily consume oil palm fruit, suggesting it is valuable to primates in general [McKinney, 2011; Estrada et al., 2012; Bryson-Morrison et al., 2016; Cancelliere et al., 2018]. The fact that females preferentially used human-modified habitats and fed on scattered, relatively scarce non-natural plants even when in near-natural forests suggests that the regular and large inclusion of non-natural foods in the diet was a result of females seeking those foods.

Blue monkeys may readily use non-natural foods not only because they were available, but also because they also provided similar access to nutritional space as natural foods. The Protein:Carb:Lipid ratio for mean caloric intakes for the three groups were similarly positioned in nutritional space, as well as occupying a position well within the shared nutritional space of non-natural and natural foods [Chap 2,3]. This overlap among mean daily nutrient intake, non-natural food nutritional space, and natural food nutritional space indicated that a blue monkey could presumably consume natural *or* non-natural *or* a mixture of both types of foods and still arrive at the mean daily diet intake. One must be cautious in interpreting RMTs, however, as

they do *not* show foods' relative availabilities to the consumer. Specifically, they include no information on availability in the habitat (e.g. seasonal or spatial variation), nor availability adjusted to a monkey's digestive system (e.g. a mature leaf might occupy a similar position as a fruit in the RMT, but the leaf's high fiber content limits the nutrients that an animal can extract). Also, indigestible fiber has a dilution effect on the nutrient content of foods, so two foods can have similar relative proportions of macronutrients, but one food may be much less nutrient dense (because of fiber content) and therefore of lower relative value to the monkey.

The finding that many non-natural foods may not be nutritionally distinct from natural foods might lead one to hypothesize that restriction to human-modified landscapes might not affect species persistence for blue monkeys in Kakamega Forest. However, the majority of their energy and nutrients came from natural food items. To date, no study has examined the population persistence of wild-living primates restricted to non-natural foods. It may be that other important nutrients, such as micronutrients (e.g. copper intake for redtail monkeys, *Cercopithecus ascanius*; Rode et al., 2006), are not available in sufficient quantities in non-natural foods (and especially in human-derived foods that are highly-processed like sweets or bread). There are also other factors related to the likelihood of persistence in human-modified habitat that I did not address in this study, including increased predation risk and the suitability of such habitat for other activities like sleeping and resting [Estrada et al., 2012]. Primates may be more susceptible to disease and parasites when inhabiting human-modified and fragmented forests [Johns, 1985; Chapman et al., 2005a; Gillespie & Chapman, 2008; Mbora et al., 2009; Young et al., 2013; Estrada et al., 2017]. Anecdotal evidence suggests that blue monkeys face a greater risk of predation by humans in modified habitats in Kakamega Forest [Cords, 2014].

In conclusion, exploring the use of non-natural foods by a primate with a flexible diet, including groups with differential access to such foods, showed that groups differed in how much they used non-natural foods yet all were able to achieve a similar nutrient balance, even over the course of months [Chap 3]. Kakamega Forest, and other regenerating forests, represent a conservation opportunity [Chazdon, 2014]. As human-modified habitat (and the non-natural food resources it contains) becomes more prevalent, studies like this one will provide species- and habitat- specific data that may allow accurate predictions of population trends in the face of potential extinction and predictions of the ecological significance of regenerating forests [Gardner et al., 2009; Estrada et al., 2017]. This study's results shed light on possible applications for conservation and management policies. Plans could prioritize cultivation and regeneration of human-modified landscapes using non-natural, fast-growing species that are known to be important (in terms of caloric and nutritional contribution) food resources for the population in question. Also, if a human-modified landscape supports multiple purposes (e.g. modified forest serving as a spillover habitat for animals and providing light timber extraction), management can ensure loggers target non-important (i.e. non-food) trees for human use while safeguarding important food resources. Understanding the value of these landscapes from a nutritional perspective of key wildlife will be important for management to effectively allocate limited resources [Chazdon et al., 2009a; Hobbs et al., 2014a]. It seems clear that human-modified landscapes, and the non-natural food resources they provide, may have conservation value for population persistence of behaviorally flexible species such as blue monkeys. As such, these human-modified, regenerating habitats merit protection and should be recognized for their conservation potential [Hobbs et al., 2009; Edwards et al., 2011; Chazdon, 2014].

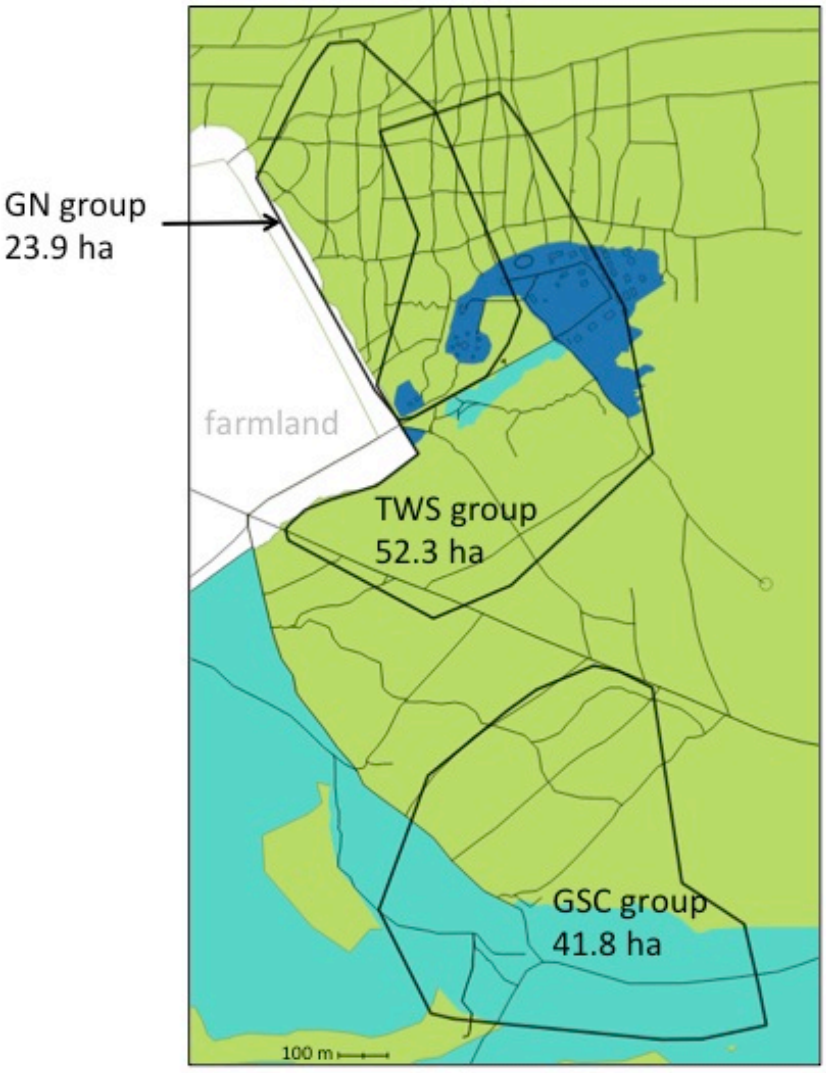


Figure 4.1. Home range size and habitat composition, showing three study groups' differential access to multiple habitat types (green=near-natural forest, turquoise=farm/plantation forest, dark blue=village forest). Bold black lines show group home range boundaries. Thin black lines show trails and roads. White space shows agricultural land (not used by monkeys). Small rectangles and ellipses represent man-made structures within the forest.

Table 4.1. Vegetation composition (basal area, cm^2 per ha) in the three habitat types.

* indicates a non-natural species (introduced or cultivated and may be naturalized [Fischer et al., 2010]). Basal areas for farm/plantation and near natural forest are derived from measurements of all trees and herbaceous plants ≥ 5 cm DBH in randomly placed 10 x 100 m transects. Basal area (BA) for each species reported as a mean (and SD) value across transects in each habitat type. % indicates percentage of transects in which species occurred. In the village forest, all trees and shrubs were measured in the part of this habitat used by TWS and/or GN group. Measurements for the village forest were scaled to represent BA as cm^2 per ha, for comparison to the two other habitat types. Means, SD and % could not be calculated given the method of enumerating the trees in the village forest.

Near natural forest (N=36 transects)				Farm/plantation forest (N=10 transects)				Village forest (total enumeration)	
Species	BA (mean)	SD	%	Species	BA (mean)	SD	%	Species	BA
Olea capensis	95882	161314	0.56	**Bischofia javanica*	336076	498451	0.9	**Cupressus lusitanica*	34184
Zanthoxylum gilletii	58934	86477	0.50	**Psidium guajava*	88612	77894	1	*Sapium ellipticum*	11280
Antiaris toxicaria	57935	97737	0.81	**Grevillea robusta*	53676	128959	0.2	*Maesopsis eminii*	8833
Funtumia africana	46525	50007	0.89	**Eucalyptus saligna*	27570	54473	0.3	*Khaya anthotheca*	7601
Prunus africana	40687	60082	0.42	**Cupressus lusitanica*	26552	72677	0.2	**Bischofia javanica*	7263
Polyscias fulva	29420	36525	0.75	*Sapium ellipticum*	17678	23658	0.6	*Funtumia africana*	7178
Trilepisium madagascariense	26735	42214	0.61	*Bridelia micrantha*	16028	15703	0.9	*Polyscias fulva*	6455
Ficus exasperata	25607	55948	0.67	*Cordia africana*	13046	41256	0.1	*Harungana madagascariensis*	4757
Ficus sansibarica	25592	153555	0.03	*Acacia abyssinica*	5720	10060	0.4	**Callistemon citrinus*	4222
Croton megalocarpus	22775	41287	0.36	*Ficus sur*	5058	12113	0.3	*Bridelia micrantha*	4181
Celtis africana	22741	51731	0.53	*Maesa lanceolata*	4981	11803	0.4	**Acrocarpus fraxinifolius*	4066
Ficus thonningii	19658	87244	0.11	*Harungana madagascariensis*	2774	4024	0.4	*Zanthoxylum gilletii*	3815
Sapium ellipticum	14288	31981	0.33	**Lantana camara*	2177	2718	0.7	*Jacaranda sp.*	3717
Maesopsis eminii	13667	33517	0.31	*Maesopsis eminii*	1419	3891	0.2	*Prunus africana*	3574
Harungana madagascariensis	6579	19447	0.17	*Acanthus pubescens*	998	1901	0.5	*Croton megalocarpus*	3205
Spathodea campanulata	6296	13507	0.28	*Kigelia africana*	928	1956	0.2	*Albizia gummifera*	2986
Cordia africana	5868	10770	0.36	*Prunus africana*	790	2134	0.2	*Olea capensis*	2278
Celtis durandii	5002	7749	0.42	*Trema orientalis*	513	1623	0.1	**Eucalyptus saligna*	2251

Near natural forest (N=36 transects)				Farm/plantation forest (N=10 transects)				Village forest (total enumeration)	
Species	BA (mean)	SD	%	Species	BA (mean)	SD	%	Species	BA
Strombosia schefleri	4932	7229	0.50	*Markhamia lutea*	471	1066	0.2	*Croton sylvaticus*	1608
Chrysophyllum albidum	4719	17516	0.11	*Spathodea campanulata*	366	838	0.2	*Cordia africana*	1443
Markhamia lutea	4564	10877	0.33	**Solanum mauritanium*	249	480	0.3	*Toona ciliata*	1425
Chaetacme aristata	4501	8561	0.53	*Albizia gummifera*	119	377	0.1	**Persea americana*	1269
Croton sylvaticus	4409	7085	0.36	*Funtumia africana*	99	312	0.1	*Spathodea campanulata*	1062
Albizia gummifera	3711	17775	0.14	*Vitex doniana*	88	279	0.1	*Margaritaria discoidea*	1015
Aningeria altissima	3460	11446	0.25	*Celtis durandii*	87	274	0.1	*Antiaris toxicaria*	766
Bridelia micrantha	3042	9869	0.17	*Croton macrostachyus*	73	230	0.1	**Psidium guajava*	688
Ficus sur	3021	16524	0.08	*Mayterius heterophylla*	26	83	0.1	*Terminalia mantaly*	660
Margaritaria discoidea	2763	7143	0.17	*Vernonia sp.*	22	70	0.1	*Ficus exasperata*	641
**Psidium guajava*	2553	10069	0.11					*Schizolobium parahybum*	565
Dracaena fragrans	2062	2493	0.64					*Hirtella zanzibarica*	380
Morus lactea	2049	6863	0.11					**Elaeis sp.,* palm	374
**Cupressus lusitanica*	1967	11804	0.03					*Acacia abyssinica*	374
Milicia excelsa	1898	7295	0.11					*Ficus thonningii*	294
Macaranga kilimandscharica	1651	8668	0.08					**Grevillea robusta*	272
Brillantaisia sp.	1375	2014	0.47					*Markhamia lutea*	261

Near natural forest (N=36 transects)			
Species	BA (mean)	SD	%
**Pinus patula*	1347	8083	0.03
Jacaranda sp.	1301	7803	0.03
Trichilia emetica	1209	4671	0.22
Bequaertiodendron oblanceolatum	880	1512	0.33
Teclea nobilis	836	3402	0.14
**Bischofia javanica*	749	4011	0.11
Oxyanthus speciosus	647	2380	0.19
Acacia abyssinica	620	2954	0.06
**Solanum mauritanium*	615	1701	0.31
Aulacocalyx diervilleoides	609	764	0.61
Vitex keniensis	608	2233	0.11
**Acrocarpus fraxinifolius*	581	2335	0.08
Ehretia cymosa	516	2809	0.06
Alangium chinense	466	2014	0.08
Croton macrostachyus	465	2789	0.03
UID tree	374	2241	0.03
Vangueria sp.	366	755	0.36

Village forest (total enumeration)	
Species	BA
Brachychiton acerifolium	234
Kigelia africana	225
Senna spectabilis	203
Casearia battiscombei	165
**Sygzium cummini*	164
Ficus sur	156
Indata abyssinica	142
Mangifera sp., mango	129
Oxyanthus speciosus	129
Erythrococca sp.	113
Celtis africana	105
Ficus cyathistipula	92
**Pinus patula*	74
Chrysophyllum albidum	69
**Solanum mauritanium*	55
Vitex doniana	47
Bersama abyssinica	32

Near natural forest (N=36 transects)			
Species	BA (mean)	SD	%
Drypetes gerrardi	334	1418	0.08
Lepidotrichilia volkensi	288	982	0.28
Dovyalis macrocalyx	287	516	0.42
Casearia battiscombei	283	1023	0.11
Bersama abyssinica	281	1016	0.08
Tabernaemontana usambarensis	230	1382	0.03
Fagaropsis angolensis	220	690	0.11
Cassipourea ruwensorensis	185	601	0.11
Kigelia africana	184	662	0.08
Deinbollia kilimandscharica	153	590	0.08
Ficus natalensis	149	892	0.03
Manilkara butugi	118	707	0.03
Monodora myristica	111	669	0.03
Mayterius heterophylla	110	316	0.17
Clerodendron silvanum	101	545	0.06
Ficus lutea	88	378	0.06
Turraea holstii	66	235	0.11

Village forest (total enumeration)	
Species	BA
Trilepisium madagascariense	32
Ficus bubu	31
Ficus lutea	29
Maesa lanceolata	22
Croton macrostachyus	22
Eriobotraya japonica	17
**Lantana camara*	16
Pavetta abyssinica	15
**Camellia sp., tea*	13
Urera trinervis	9

Near natural forest (N=36 transects)			
Species	BA (mean)	SD	%
Rothmannia urcelliformis	56	182	0.14
Flueggea virosa	55	332	0.03
Acanthus pubescens	40	144	0.08
Maesa lanceolata	36	159	0.06
Ficus cyathistipula	29	172	0.03
Erythrococca sp.	27	160	0.03
**Lantana camara*	22	75	0.08
Hippocratea africana	18	79	0.06
UID shrub	13	77	0.03
**Camellia sp.,* tea	8	49	0.03
Lepisanthes senegalensis	8	46	0.03
Scutia myrtina	7	41	0.03
Keetia gueinzii	6	34	0.03

Table 4.2. Non-natural foods of Kakamega blue monkeys, both exotic plant foods and human-derived. Within each category, foods are listed in descending order of percentage of time that subjects spent feeding on them (as a cumulative proportion of 988 hrs of feeding observations during study period). Foods are described using their scientific name when possible. Some common names are added to scientific names to add clarity. No foods are a result of crop-raiding.

Exotic plants	Percentage of time spent feeding
Bischofia javanica	10.29
Psidium guajava	5.36
Cupressus lusitanica	5.03
Solanum mauritianum	2.66
Lantana camara	2.42
Persea americana	0.31
Acrocarpus fraxinifolius	0.22
Elaeis sp., oil palm	0.20
Passiflora sp.	0.16
Eucalyptus saligna	0.15
Bidens formosa	0.07
Eriobotrya japonica	0.02
Callistemon citrinus	0.01
Calliandra gilberti	0.01
Brunfelsia pauciflora	0.01
Human-derived foods	
ugali (cooked maize flour)	0.13
Musa paradisiaca, banana	0.05
Zea sp., maize	0.03
Citrus sp., orange	0.02
Ipomoea sp., sweet potato	0.02
Citrullus sp., watermelon	0.01
Saccharum sp., sugar cane	0.01
chicken egg	0.01
Brassica sp., cabbage	<0.01
Mangifera sp., mango	<0.01

Table 4.3. Non-natural foods in the daily diet by group, showing the percentage of non-natural calories, total energy intake (kcal and g), and macronutrient intake (kcal of TNC, lipid, NDF, protein, NPE and g of NDF, ADF, ADL). All values represent grand means ± SD across 8 females per group, 24 for "population". Groups are ordered left to right by the percentage of human-modified habitat in home ranges (GSC highest).

	GSC		TWS		GN		Population	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
% (by kcal) in diet	55.0	11.2	25.4	5.3	21.8	4.9	34.1	16.9
Total energy (kcal)	411.5	131.9	232.6	117.5	133.6	55.1	259.3	155.6
NPE (kcal)	366.5	118.3	218.7	115.8	125.7	54.3	237.0	139.6
TNC (kcal)	199.9	64.3	75.1	21.3	62.3	27.9	112.4	75.2
Lipid (kcal)	117.0	36.2	116.0	97.5	31.6	13.2	88.2	70.8
NDF (kcal)	49.6	18.3	27.6	7.9	31.8	13.5	36.4	16.5
Protein (kcal)	45.0	14.4	13.9	2.9	7.9	3.2	22.3	18.6
Food (g)	157.6	54.1	61.4	17.5	53.5	21.8	90.8	58.9
NDF (g)	75.5	27.8	23.7	6.8	28.6	12.2	42.6	29.4
ADF (g)	65.8	23.9	19.9	6.6	27.0	12.0	37.6	25.6
ADL (g)	28.8	10.4	9.2	3.0	13.5	6.3	17.2	11.0

Table 4.4. Significant differences in daily intake of non-natural food by females in different groups. Linear mixed models tested differences between all pairs of groups (by adjusting the baseline predictor, indicated in parentheses). All models had Subject ID as a random effect and N=371 daily intakes. Only group pairs with significant differences are presented here. * indicates significance. Intakes are ordered by descending R^2 values, which are pseudo- R^2 [Lefcheck, 2016].

Non-natural food intake	Predictor	Estimate	SE	95% CI			df	t-value	p-value	fixed effects R^2	random effects R^2
Protein (kcal, DW)	Group (GSC)									0.26	0.02
	GN*	-37.09	4.27	-45.23	–	-28.94	20.39	-8.69	2.72E-08		
	TWS*	-31.09	4.27	-39.23	–	-22.95	20.39	-7.28	4.29E-07		
	Intercept*	44.98	3.02	39.22	–	50.75	20.50	14.88	1.86E-12		
NDF (g, DW)	Group (GSC)									0.20	0.07
	GN*	-46.82	8.90	-63.80	–	-29.84	20.67	-5.26	3.41E-05		
	TWS*	-51.62	8.90	-68.60	–	-34.64	20.67	-5.80	9.89E-06		
	Intercept*	75.33	6.30	63.32	–	87.35	20.74	11.96	9.07E-11		
ADF (g, DW)	Group (GSC)									0.19	0.07
	GN*	-38.77	7.88	-53.82	–	-23.73	20.67	-4.92	7.60E-05		
	TWS*	-45.76	7.88	-60.80	–	-30.71	20.67	-5.80	9.83E-06		
	Intercept*	65.67	5.58	55.03	–	76.32	20.74	11.77	1.22E-10		
TNC (kcal, DW)	Group (GSC)									0.18	0.03
	GN*	-137.51	20.92	-177.43	–	-97.59	20.55	-6.57	1.84E-06		
	TWS*	-124.23	20.92	-164.17	–	-84.32	20.55	-5.94	7.44E-06		
	Intercept*	199.45	14.81	171.20	–	227.73	20.65	13.46	1.08E-11		
Food (g, DW)	Group (GSC)									0.18	0.05
	GN*	-104.05	17.42	-137.29	–	-70.81	20.61	-5.97	6.78E-06		
	TWS*	-95.84	17.42	-129.09	–	-62.62	20.61	-5.50	1.97E-05		
	Intercept*	157.29	12.33	133.78	–	180.83	20.70	12.76	2.85E-11		

Non-natural food intake	Predictor	Estimate	SE	95% CI			df	t-value	p-value	fixed effects R^2	random effects R^2
ADL (g, DW)	Group (GSC)									0.15	0.06
	GN*	-15.27	3.58	-22.10	–	-8.45	20.65	-4.27	3.53E-04		
	TWS*	-19.55	3.58	-26.37	–	-12.72	20.65	-5.46	2.14E-05		
	Intercept*	28.73	2.53	23.90	–	33.57	20.72	11.35	2.37E-10		
Energy (kcal, DW)	Group (GSC)									0.08	0.01
	GN*	-277.79	53.21	-379.35	–	-176.23	20.85	-5.22	3.65E-05		
	TWS*	-176.59	53.21	-278.22	–	-75.09	20.85	-3.32	3.29E-03		
	Intercept*	410.42	37.69	338.52	–	482.38	20.99	10.89	4.29E-10		
NPE (kcal, DW)	Group (GSC)									0.07	0.01
	GN*	-240.70	50.17	-336.47	–	-144.94	20.91	-4.80	9.77E-05		
	TWS*	-145.46	50.17	-241.29	–	-49.75	20.91	-2.90	0.01		
	Intercept*	365.43	35.53	297.62	–	433.28	21.05	10.28	1.15E-09		
NDF (kcal, DW)	Group (GSC)									0.05	0.05
	GN*	-17.90	6.88	-31.03	–	-4.77	20.60	-2.60	0.02		
	TWS*	-21.91	6.88	-35.04	–	-8.78	20.60	-3.18	4.54E-03		
	Intercept*	49.53	4.87	40.24	–	58.83	20.69	10.17	1.68E-09		
Lipid (kcal, DW)	Group (GN^A)									0.02	0.00
	GSC*	85.27	34.53	17.69	–	152.84	371.60	2.47	0.01		
	TWS*	85.98	34.46	18.54	–	153.41	371.60	2.50	0.01		
	Intercept	31.32	24.37	-16.37	–	79.00	371.60	1.29	0.20		

[A] GN shown as reference group to present significant difference relative to GSC and TWS. For all other pairwise comparisons, GN and TWS did not significantly differ from each other.

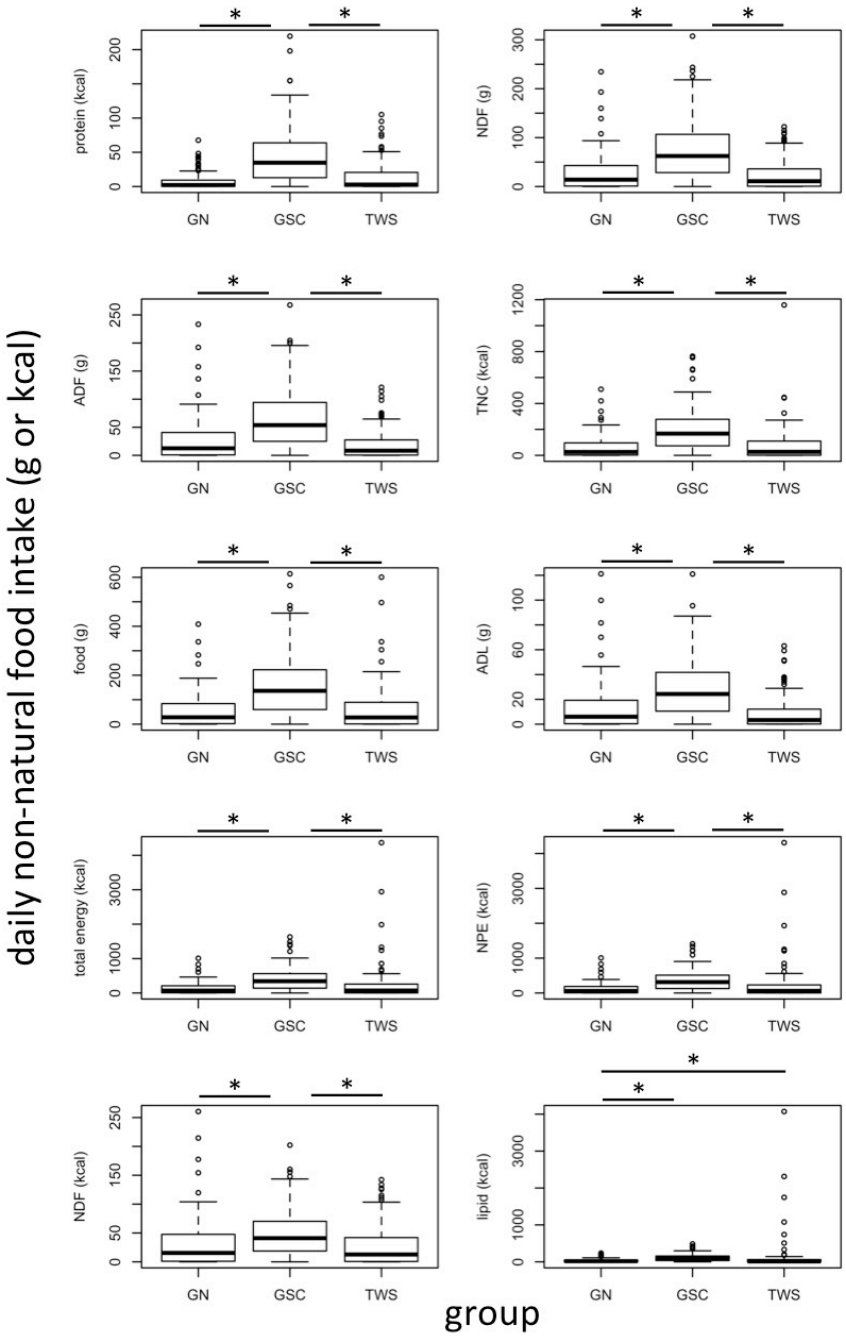


Figure 4.2. Boxplots for daily non-natural nutrient and energy intake differences for females in different groups. Linear mixed models tested for group differences in daily intake (Table 4.4), with significant differences shown by a black bar with asterisk. Boxplots show median and interquartile range. Whiskers represent the most extreme data point, no more than 1.5 * IQR away from the box. Outliers are data points beyond the whiskers.

Table. 4.5. Likelihood ratio tests for testing the significance of group as fixed effect in predicting non-natural nutrient and energy intake. Linear mixed models included subject ID as random effects.

	X^2	df	p-value
Protein (kcal)	39.15	2	3.15E-09
NDF (g)	25.99	2	2.28E-06
ADF (g)	25.21	2	3.35E-06
TNC (kcal)	30.03	2	3.01E-07
Food (g)	27.13	2	1.29E-06
ADL (g)	22.65	2	1.21E-05
Energy (kcal)	20.30	2	3.90E-05
NPE (kcal)	17.95	2	1.26E-04
NDF (kcal)	10.48	2	0.01
Lipid (kcal)	8.19	2	0.02

Table 4.6. Important non-natural food items by group, ordered left to right by the percentage of human-modified habitat in home ranges (GSC highest). Important foods were those contributing ≥1% of calories consumed by all females in a group during the study period (Jan-Sep 2015). % indicates the percentage of calories contributed by a food item. Rank indicates the importance of a food to each group, based on a ranking of % and including both natural and non-natural foods. For example, *Psidium guajava* fruit is the most important food item for GSC females and 46% of all calories came from that fruit.

Rank	GSC group	%	Rank	TWS group	%	Rank	GN group	%
1	*Psidium guajava* fruit	45.7	1	*Elaeis sp*. (oil palm) fruit	13.9	1	*Bischofia javanica* fruit	15.5
2	*Bischofia javanica* fruit	10.2	2	*Psidium guajava* fruit	8.2	5	*Solanum mauritanium* fruit	3.3
11	*Solanum mauritanium* fruit	1.0	3	*Bischofia javanica* fruit	6.9			
			15	*ugali*	1.8			
			17	*Solanum mauritanium* fruit	1.4			
			19	*Musa paradisiaca* fruit	1.2			

Table 4.7. Cross-group comparison of habitat representation in the home range and mean ± SD percentage of day spent in different habitat types. Groups are ordered top to bottom by the percentage of near-natural forest in home ranges (GN highest). % daily use is the grand mean ± SD percentage of daily time females spent in a habitat type (N=8, based upon GPS records). SR=selection ratios (% habitat use divided by % habitat composition in the home range), shown as grand means (N=8).

	Near-natural forest			Village Forest			Farm/plantation forest		
	% home range	% daily use	SR	% home range	% daily use	SR	% home range	% daily use	SR
GN	92.1	93.1 ± 2.9	1.0	7.9	6.9 ± 2.9	0.9	0.0	-- --	--
TWS	85.2	77.1 ± 4.2	0.9	12.6	21.6 ± 4.7	1.7	2.2	1.3 ± 0.7	0.6
GSC	55.6	40.5 ± 8.1	0.7	0.0	-- --	--	44.4	59.5 ± 8.1	1.3

Table 4.8. Model (zero-inflated beta regression) for relationship between percentage of day spent in human-modified habitat and percentage of daily calories sourced from non-natural foods. * indicates significance. pseudo-R^2=0.44.

	Estimate	SE	t-value	p-value
Mu formula with logit link function				
% time*	2.14	0.18	11.91	<2e-16
Intercept*	-1.27	0.09	-14.42	<2e-16
Nu formula with logit link function				
% time*	-7.19	1.82	-3.94	9.69e-05
Intercept*	-0.96	0.18	-5.30	2.04e-07

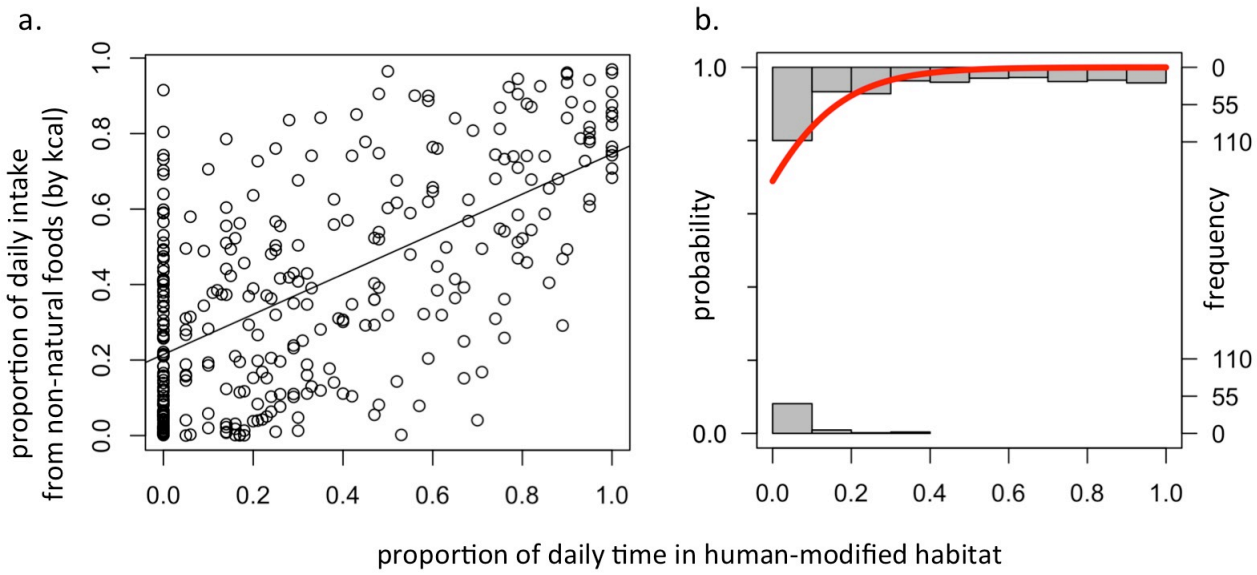
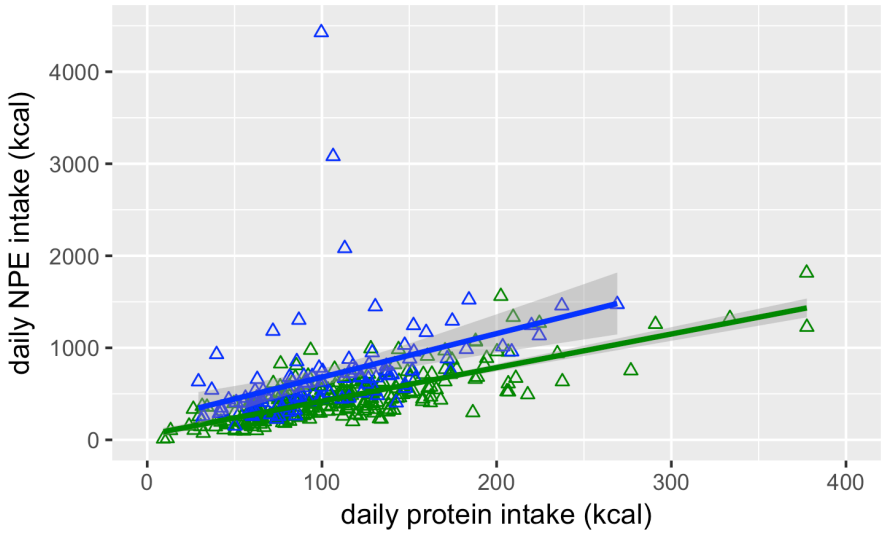


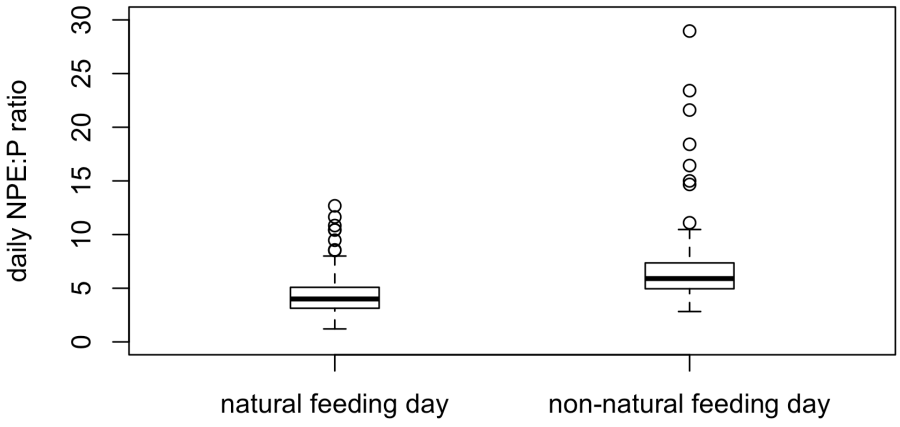
Figure 4.3. Positive relationship between consumption of non-natural food and use of human-modified habitat. a) shows the OLS linear relationship between the percentage of daily intake (kcal) from non-natural foods for values >0 and the percentage of the daily time in human-modified habitat. A triangle represents a female-day (N=319 female-days). b) shows the relationship of NOT consuming non-natural food in a given day (0 on the y axis) and consuming non-natural food in a given day (1 on the y-axis) with the proportion of time spent in human-modified habitat. The red line shows the positive relationship between the dependent and independent variables. The gray histogram columns indicate the frequency of 0s and 1s as the percentage time spent in human-modified habitat changes (N=371 female-days). I made the graphic in R using the package "popbio" [Smart et al., 2004; Stubben & Milligan, 2007; R Core Team, 2016]

Table 4.9. Linear mixed model for the relationship between type of feeding day and NPE:P ratio or protein intake. Baseline for type of feeding day was non-natural (i.e. natural feeding days=0 and non-natural feeding model=1 in the model). * indicates significance.

Response variable	Fixed effect	Estimate	SE	95% CI	df	t-value	p-value	Fixed effects R^2	Random effects R^2
NPE:P ratio	Type of feeding day: (non-natural)*	3.33	0.4	2.42 − 4.09	288.31	8.28	4.88E-15	0.18	0.03
	Intercept*	4.17	0.43	3.2 − 5.09	2.15	9.7	8.16E-03		
Protein (kcal)	Type of feeding day: (non-natural)	-5.8	6.01	-17.57 − 5.96	369	-0.97	0.33	2.52E-03	0
	Intercept*	109.62	3.3	103.09 − 117.71	369	33.22	<2e-16		



a.



b.

Figure 4.4. Daily NPE:P balancing when feeding on mostly natural versus non-natural foods. Females consumed more non-protein energy (NPE) per unit of protein (P) on days when they fed primarily on non-natural foods. In a) a blue triangle represents a day when a female consumed a diet with > 50% of calories sourced from non-natural foods (i.e. non-natural feeding days). A green triangle represents a day when a female consumed a diet with >50% of calories from natural foods (i.e. natural feeding days). Lines indicate OLS linear relationships between variables while gray envelope indicates 95% confidence interval. In b) the boxplot shows that mean NPE:P ratio of non-natural feeding days was higher than natural feeding days (see Results for model details). See Figure 4.2 for boxplot explanation.

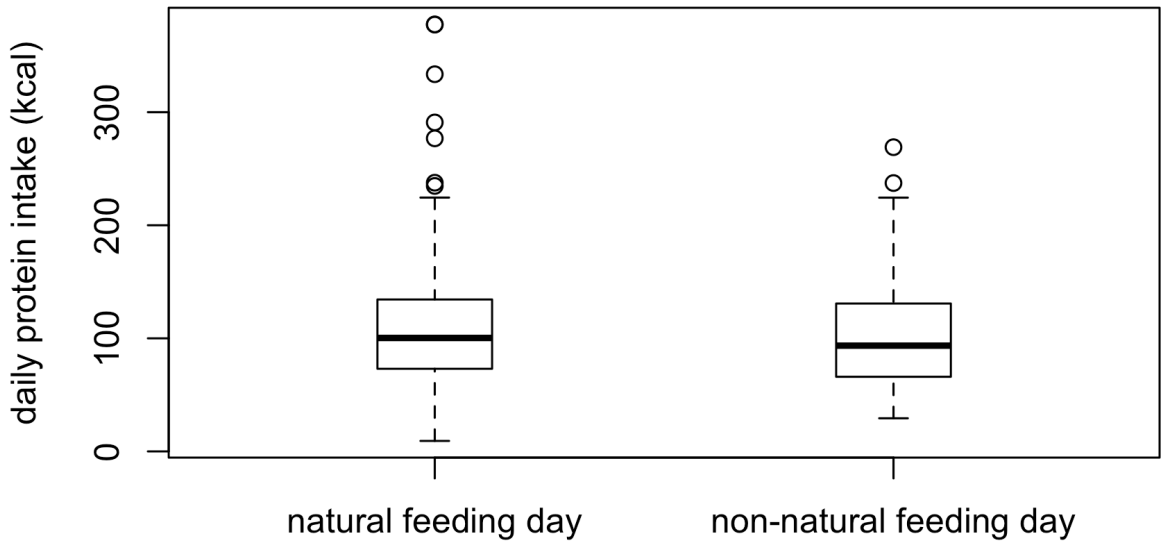


Figure 4.5. Protein intake when feeding on mostly natural vs. non-natural foods. A non-natural feeding day represents a day when a female consumed a diet with > 50% of calories sourced from non-natural foods. On natural feeding days, a female consumed a diet with >50% of calories from natural foods. Females did not consume more protein (kcal) on a daily basis on days when they fed primarily on natural vs. non-natural foods. See Figure 4.2 for boxplot explanation.

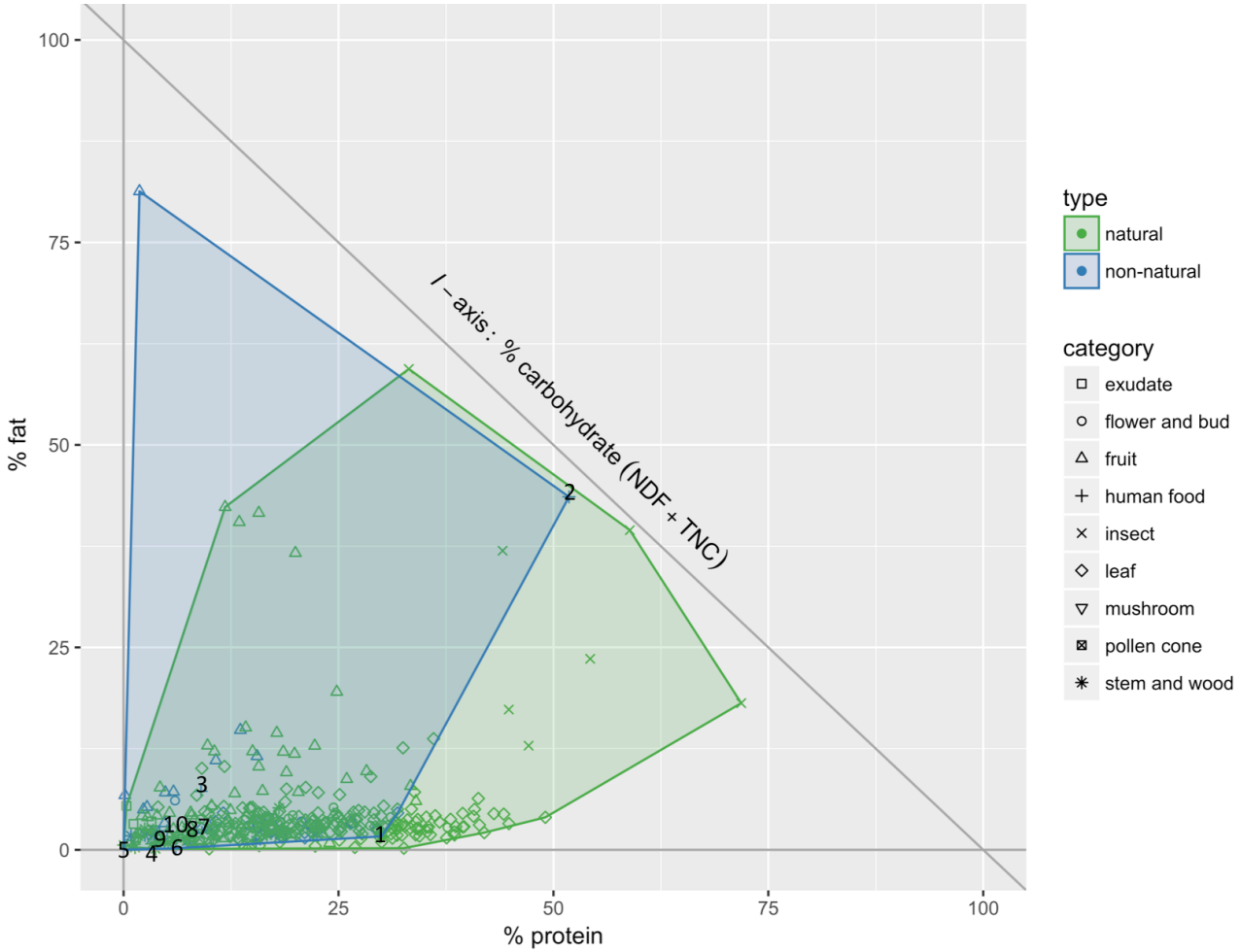


Figure 4.6. RMT of natural versus non-natural food nutritional spaces, demonstrating the nutritional space for natural and non-natural foods. A point represents a species- specific food item, with its position determined by its relative proportions of fat, protein, and carbohydrates (dry matter, gram basis). Human derived foods are labeled with numbers as follows: 1=cabbage,

2=chicken egg, 3=maize, 4=orange, 5=sugar cane, 6=sweet potato, 7=*ugali*, 8=watermelon, 9=banana, 10=mango. Symbol type indicates food item type (e.g. fruit or human food). The topmost blue triangle (upper left corner) represents oil palm fruit. Polygons represent the *nutritional space* occupied by either non-natural foods (blue) or natural foods (green). A blue monkey can consume a diet that falls anywhere within the nutritional space bounded by a polygon via consuming a mixture of the different foods composing the polygon.

CHAPTER 5. CONCLUSION

The previous chapters provide new insights on the diet and nutritional ecology of a generalist-feeding primate, the blue monkey (*Cercopithecus mitis*). This study, based on 371 full-day focal follows from 24 adult females in 3 groups, as well as vegetation surveys to assess the availability of food, and laboratory analysis of 352 food samples and 205 fecal samples, represents one of the most comprehensive data sets relevant to the nutritional ecology of primates, and certainly among guenons. This concluding chapter reviews the main results of each chapter, and highlights overall conclusions.

Chapter 1 reviewed the components of nutrition, the relationship between diet and digestive morphology in primates, and the value of the Geometric Framework (GF) to nutritional ecology studies. Most knowledge of primate nutritional needs stems from limited studies of captive populations. The requirements of wild populations are not well known (but see [Conklin-Brittain et al., 1998a, 1998b; Norconk & Conklin-Brittain, 2004; Sterling et al., 1994]) and likely to differ from captive ones. What primates actually consume is a product of many interconnected environmental (abiotic and biotic) factors and physiological factors, some of which include nutrient needs, morphology, and adaptations in the digestive tract. Studies of nutritional ecology necessarily involve these interconnected relationships and also place them in the context of a primate's food environment [Raubenheimer et al., 2009]. Additionally, these relationships are dynamic, adding to their complexity: the nutrient needs of consumers change over different time scales (i.e. short term response to last meal versus long term response to life history stage) and there is spatiotemporal variation in food environments. The GF is a powerful way to quantify

dietary behavior, an animal's feeding strategy and its effectiveness in balancing changing nutritional needs in context of its habitat.

Chapter 2 characterized the diet of subjects, in terms of food selection and daily nutritional intake. Similar to most previous studies, I found that fruit was the largest constituent of the diet (in terms of both time and energy) and young leaves were the second largest constituent. Many species-specific fruits, as well as young leaves, were important food items (contributing >1% of total caloric intake by group). Subjects positively selected more than half of the fruits that were monitored for phenology and many of these fruits were also important food items. In contrast, many important species of young leaves were eaten in proportion to their availability, or even less often. Subjects in different groups exhibited many dietary similarities. Dietary percentages of food item types (fruit, young leaves), caloric contribution of all important foods, and energy, ash, NPE, and protein intake were similar for subjects across groups. Diet and nutrient intake were related to food availability. When fruit was more available, it constituted a larger proportion of dietary intake and its absolute intake (kcal) increased, whereas the absolute intake of young leaves decreased. When fruit availability was low, subjects consumed more structural carbohydrates (as measured by neutral detergent fiber, acid detergent fiber, and acid detergent lignin). These results on dietary patterns and food availability support and expand upon prior studies that demonstrated that blue monkeys have broad diets, prefer fruit, and rely on young leaves as fallback foods [Cords, 1987; Foerster et al., 2011; Lawes et al., 1990]. These results hold throughout their range and regardless of spatiotemporal variation in food availability [Chapman et al., 2002; Coleman & Hill, 2014; Lawes et al., 2013]. Also, I explored one possible correlate of foraging behavior: an individual's daily path length (DPL). I found that higher proportions of fruit in the diet (by kcal) were associated with lower DPLs and there was no

evidence that DPL related to group size. Important fruits ripened *en masse*, which encouraged females to spend most of their feeding time in a few trees; thus they traveled less on a daily basis. The absence of relationship between group size and DPL suggests that females may use feeding strategies (e.g. spreading out when foraging) to avoid within-group scramble competition over food. Finally, the GF analysis using RMTs showed that the possible dietary space of the population was broad, yet average diets converged in nutrient space (similar across groups and within the population as a whole). Diets were also different from those expected if foods had been consumed in proportion to their availability. Group differences in the breadth and relative importance of food items likely reflected home range differences in habitat composition and food distribution. Diverse diets providing access to broad nutritional space indicated that blue monkeys were food composition generalists, although they actively regulated nutrient consumption to converge in nutrient space, and thus were nutrient intake specialists. An examination of a multidimensional nutritional niche clarifies how diet selection relates to nutrient intake, and may even reveal behavioral feeding adaptations that would otherwise remain opaque. Further, their specific multidimensional nutritional niche (i.e. flexible feeding with broad diets that converges on similar nutrient intake) may explain the species' widespread African distribution and their persistence in human-modified habitats.

Chapter 3 demonstrated that blue monkey females prioritized daily protein intake, which varied least in daily consumption compared to other nutritional components. Also, on average, they balanced daily NPE to P intake in a 3.8 to 1 ratio. As expected when protein is prioritized, they allowed the non-protein energy to protein (NPE:P) ratio to increase when the percentage of protein in the diet was lower than average and vice versa. Environmental and dietary factors were significant predictors of variation in NPE:P ratio. Subjects had higher daily ratios when

they spent less time in near-natural forest and when the diet included a higher percentage of fruit. Reproductive demand and social factors (dominance rank) did not relate to daily NPE:P ratio. None of the above factors related significantly to protein intake. Also, dominance rank did not affect deviation (absolute or directional) from daily mean NPE:P ratio or protein intake. Dominance rank was, however, negatively related to daily dietary breadth. Females' ability to adjust daily dietary breadth may be a feeding strategy to cope with social constraints when feeding and thus explain the absence of rank effect on nutritional strategies. Overall, these findings are in agreement with the larger picture that regardless of environmental, social, or physiological differences, all females in the population prioritized and succeeded in consuming their daily target protein intake. Subjects seem to permit less variation in protein intake than NPE:P ratio. Despite variation observed in *daily* NPE:P ratios, subjects balanced *cumulative* NPE:P ratios that were remarkably similar to one another: in short, the cumulative ratio was tightly regulated across subjects and groups in the study population, and regardless of dominance rank. Overall, this evaluation of how multiple factors influenced the nutritional strategy of blue monkeys showed that they are generalist, flexible feeders that successfully navigate heterogeneous landscapes, social constraints, and reproductive demands to adhere closely to their particular nutritional strategy.

Chapter 4 showed that blue monkey females incorporated a substantial amount of non-natural food (human-derived foods and exotic plants) into their diets, with five species of exotic plants dominating non-natural food intake. Overall, the monkeys consumed approximately a third of their daily calories from non-natural foods, but this figure varied by group. In the group with the highest percentage of human-modified habitat in its range, subjects used non-natural foods most extensively, and used them as a source of more than half their calories. Females of

two groups showed a preference for human-modified habitats, while those in the third group used habitat types in proportion to their representation in the home range. When subjects spent time in human-modified habitat, they consumed almost half of their calories from non-natural foods. Even when they did not use human-modified habitats, they still derived approximately a fourth of their calories from non-natural foods. Blue monkeys may exploit non-natural foods because they provide similar access to nutritional space as natural foods. One exception was an exotic oil palm, *Elaeis sp.*, fruit, which provided access to nutritional space characterized by high fat content; it proved to be an attractive resource to the monkeys.

Subjects had a higher NPE:P ratio when they consumed a daily diet that was mostly non-natural (in terms of the source of calories), compared to diets that were mostly natural. They also showed more variation in NPE:P on non-natural vs. natural feeding days. Despite variation in the NPE:P ratio, subjects showed little variation in absolute protein intake as a function of non-natural feeding. This consistency of protein intake again agreed with the overall picture that they capitalized on non-natural resources to maximize NPE intake as long as they were able to consume a threshold amount of protein. It remains unclear whether these monkeys gain fitness benefits from their ability to consume diets with variable NPE:P ratios when presented with energy-rich non-natural foods.

In summary, results from this study highlight how feeding flexibility helps one primate, the blue monkey, achieve consistent, precise nutritional goals. Across groups that had differential access to various habitat types, members of this population exploited hundreds of food items to converge on similar nutrient intakes in terms of protein and cumulative NPE:P balance. This pattern of generalist-style food consumption but active regulation to a similar balance in nutrient space illustrates the value of considering a multidimensional nutritional niche to describe diet on

various scales; different levels of a diet (i.e. food versus nutrient) may relate to one another in unexpected ways. Dietary and nutritional patterns can also be described on different timescales. On a daily basis, subjects prioritized protein intake, regardless of potential influences from environmental, social or physiological factors. They balanced a daily NPE:P ratio to a lesser extent, taking advantage of high NPE foods like oil palm fruit. On a longer term basis (i.e. over the 8 study months), however, subjects tightly balanced cumulative NPE:P intake, regardless of daily fluctuations that were linked to environmental (time spent in habitat types) and dietary factors (percentage of fruit in diet and natural versus non-natural food). There was no evidence that reproductive demand or dominance rank affected nutritional strategy, which suggests that these monkeys may adjust their feeding behavior (e.g. spreading out or adjusting dietary breadth) to cope with social challenges such as within-group feeding competition. Also, the lack of relationship between reproductive demand and nutritional strategy suggests that, over an evolutionary timescale, blue monkeys evolved a capital breeding strategy that relies on stored energy and nutrient reserves in the body, rather than current intake, to successfully reproduce [Janson & Verdolin, 2005]. This view coincides with the proposal that their relatively long inter-birth intervals may be an additional evolved trait to cope with reproductive demands by allowing longer periods to accumulate energetic and nutritional reserves [Cords, 2012]. Finally, the prevalence of NPE:P balancing in this and other studies of primate nutritional ecology suggests that the diverse dietary strategies of primates may have evolved to allow them to adhere to a balance of NPE:P.

Some primates, such as blue monkeys, persist and may even thrive in some human-modified forests, such as Kakamega Forest. The blue monkeys in the study area regularly and heavily used human-modified habitats, as well as non-natural food resources found in less

modified forest areas. Additional studies of primates in human-altered habitats, especially through the lens of key resources such as food (and the nutrients they contain), will help researchers to understand and even predict population-level responses to human modification and thereby to allocate conservation efforts accordingly. Data on a species' behavioral decisions regarding food intake may even allow forest managers and conservationists to manipulate their food landscape strategically to ensure or promote persistence within an ecosystem [Blumstein & Fernández-Juricic, 2010]. This study supports the idea that human-modified habitats, such as regenerating forests, can contribute to, and possibly be important to, the persistence of this species and others that have a similar ecology [Chazdon, 2014; Edwards et al., 2011; Hobbs et al., 2009].

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APPENDIX

Appendix I. Nutritional values of foods eaten by blue monkeys in this study, including plant-based foods and insect morphotypes. Plant-derived foods are listed first, alphabetically by family, species and part, then mushroom and insect morphotypes are listed, alphabetically. All numbers represent percentages on a dry matter basis. Insect morphotype values were calculated via wet chemistry methods performed by P. Wakaba from Kenya Agricultural & Livestock Research Organization, Muguga campus. Insect ADL values were an estimated value of chitin percentage.

Scientific name	Part	Processing	Dry Matter	Lipid	NDF	ADF	ADL	CP	AP	Ash	TNC
Acanthaceae											
Brillantaisia sp.	stem		95.1	0.6	67.3	57.0	16.1	10.3	7.2	12.2	12.7
Brillantaisia sp.	young leaf		93.3	2.7	44.1	27.6	13.9	37.3	27.6	15.4	10.3
Justicia sp.	mature leaf		92.4	1.9	36.6	26.9	14.8	30.5	21.4	16.0	24.7
Justicia sp.	young leaf		93.4	2.8	33.1	23.8	11.5	25.9	21.3	15.7	28.7
Mimulopsis solmsii	stem		94.7	0.1	74.1	61.3	13.0	5.6	3.6	3.0	19.1
Mimulopsis solmsii	young leaf, mature leaf		92.6	1.5	41.3	25.1	12.8	25.1	19.9	13.0	25.7
Thunbergia alata	flower		94.0	2.8	34.9	25.6	6.7	21.8	18.9	13.5	30.1
Thunbergia alata	young leaf		93.2	2.5	50.8	27.7	12.2	27.5	25.3	20.1	5.2
Amaranthaceae											
Achyranthes aspera	young leaf		92.6	1.6	47.1	17.7	4.3	31.3	29.7	17.1	4.9
Cyathula sp.	mature leaf	no petiole	92.6	1.8	46.1	14.5	7.4	34.2	32.1	17.5	3.3
Cyathula sp.	young leaf		93.6	0.2	49.7	23.5	10.6	35.3	28.2	14.2	8.4
Annonaceae											
Monodora myristica	young leaf		93.4	2.7	53.0	34.1	10.5	25.2	20.4	12.0	11.9
Apocynaceae											

Scientific name	Part	Processing	Dry Matter	Lipid	NDF	ADF	ADL	CP	AP	Ash	TNC
Funtumia africana (latifolia)	flower bud, flower		92.8	2.6	35.7	28.0	15.2	17.0	12.8	6.0	43.0
Funtumia africana (latifolia)	fruit	fresh seeds	98.3	40.2	16.4	8.7	4.2	15.9	15.2	3.3	24.9
Funtumia africana (latifolia)	fruit	dry seeds	96.7	35.2	24.5	14.7	7.3	21.0	19.2	3.8	17.2
Funtumia africana (latifolia)	stem		94.6	2.3	45.9	35.9	7.8	19.3	17.4	6.3	28.2
Funtumia africana (latifolia)	unripe fruit		95.0	6.7	31.2	21.8	10.9	16.2	12.4	4.2	45.5
Funtumia africana (latifolia)	young leaf		93.2	3.6	38.1	25.9	12.9	18.9	15.5	8.0	34.8
Tabernaemontana usambarensis (ventricosa)	young leaf		94.8	6.3	32.9	28.1	11.6	31.5	29.9	12.2	19.2
Araliaceae											
Polyscias fulva	bark		92.4	1.6	66.6	52.8	22.1	3.6	1.6	7.0	23.2
Polyscias fulva	exudate		94.4	3.3	2.0	0.5	0.3	3.1	3.1	5.0	86.6
Polyscias fulva	flower		92.6	1.6	31.5	22.8	9.7	14.8	12.0	3.0	51.9
Polyscias fulva	flower bud		92.9	2.1	39.5	25.8	10.0	15.2	12.9	4.9	40.4
Polyscias fulva	fruit		91.8	4.0	40.8	34.1	19.4	10.6	7.5	4.9	42.7
Polyscias fulva	leaf bud		93.5	3.6	49.0	35.5	14.6	19.0	14.3	6.3	26.8
Polyscias fulva	stem		94.6	0.7	80.2	63.8	14.3	3.1	1.2	<0.1	17.9
Polyscias fulva	young leaf		93.9	1.5	60.3	42.3	17.0	14.9	11.6	6.8	19.8
Arecaceae											
Elaeis sp., oil palm	fruit		99.1	80.9	13.5	5.0	2.2	2.1	1.8	0.5	3.3
Asparagaceae											
Dracaena fragrans	flower		93.9	4.9	20.4	12.9	5.6	24.5	23.0	6.0	45.7
Dracaena fragrans	ripe fruit		92.0	3.0	19.9	15.1	3.0	11.2	9.9	18.8	48.4
Dracaena fragrans	stem		94.5	0.9	69.0	58.4	12.2	7.0	5.0	4.3	20.8
Dracaena fragrans	young leaf		94.0	2.7	53.8	43.6	19.9	25.0	20.0	14.6	12.5
Asteraceae											
Bidens formosa	flower		93.8	3.2	30.8	22.0	9.0	21.7	18.6	10.1	37.5
Bidens formosa	stem		94.9	1.7	41.0	32.1	5.9	19.6	18.1	20.5	19.7
Erlangea sp.	mature leaf	no petiole	93.3	2.5	43.4	31.5	19.4	27.5	20.5	11.4	23.3
Erlangea sp.	young leaf	no petiole	93.1	2.6	38.3	27.2	14.6	32.0	28.3	12.5	20.2
Melanthera scandens	mature leaf		92.6	1.8	43.7	28.7	12.4	21.5	18.4	18.5	19.7

Scientific name	Part	Processing	Dry Matter	Lipid	NDF	ADF	ADL	CP	AP	Ash	TNC
Melanthera scandens	young leaf		92.9	1.6	42.1	27.5	15.9	29.7	27.5	14.1	15.3
Vernonia sp.	mature leaf	no petiole	92.6	2.6	43.5	30.4	18.0	26.2	22.4	13.3	19.9
Balsaminaceae											
Impatiens sp.	fruit		92.6	3.3	39.5	33.1	21.7	18.6	13.7	8.8	34.7
Bignoniaceae											
Kigelia africana	young leaf		92.7	1.3	49.1	38.1	16.3	17.6	11.8	11.9	26.9
Kigelia africana	young leaf, mature leaf		92.0	0.1	46.9	39.5	16.5	15.5	8.8	13.0	32.7
Markhamia lutea (platycalyx)	stem		93.9	1.3	76.9	63.8	23.6	14.9	9.7	8.4	4.6
Markhamia lutea (platycalyx)	young leaf		93.9	3.5	34.8	18.3	9.3	36.8	32.1	6.3	23.3
Spathodea campanulata (nilotica)	flower		95.9	1.8	37.2	29.7	15.6	16.2	7.8	10.8	42.5
Spathodea campanulata (nilotica)	fruit		92.3	14.6	54.7	48.9	17.0	16.2	13.7	3.4	13.6
Spathodea campanulata (nilotica)	leaf bud		93.7	2.2	41.4	34.3	20.0	24.6	14.9	8.9	32.6
Spathodea campanulata (nilotica)	stem		94.4	0.3	72.7	63.1	18.0	4.6	1.3	4.8	20.9
Spathodea campanulata (nilotica)	young leaf		93.3	3.1	37.6	30.9	20.0	23.8	23.8	2.4	33.1
Boraginaceae											
Ehretia cymosa	stem	young	92.9	1.6	45.6	32.1	8.5	17.7	14.6	12.4	25.7
Ehretia cymosa	young leaf		91.9	3.1	33.1	22.7	10.8	26.3	21.5	7.9	34.3
Cannabaceae											
Celtis africana	fruit		92.2	0.6	32.3	23.4	7.7	19.5	17.5	27.0	22.6
Celtis africana	leaf bud		94.3	3.5	30.5	16.8	7.4	47.0	42.7	13.0	10.3
Celtis africana	mature leaf		92.4	3.2	40.7	17.0	7.6	22.9	22.9	15.2	18.1
Celtis africana	young leaf		92.8	2.5	35.9	22.2	12.9	30.1	26.7	12.3	23.2
Celtis durandii	young leaf		92.3	2.8	37.1	20.9	6.4	32.7	29.3	8.2	22.7
Trema guineensis (orientalis)	fruit		94.7	11.3	44.8	40.8	26.6	19.3	17.4	18.5	20.0
Trema guineensis (orientalis)	leaf bud		92.3	2.5	35.0	32.8	18.1	22.2	15.9	8.7	38.0
Trema guineensis (orientalis)	mature leaf		92.1	4.5	32.2	23.6	12.3	16.2	12.7	15.4	35.3
Trema guineensis (orientalis)	young leaf		92.5	3.1	31.9	22.7	12.4	20.0	16.6	8.4	39.9
Capparaceae											
Ritchiea albersii	flower		94.5	2.5	19.2	13.3	3.0	35.3	34.2	9.3	34.8

Scientific name	Part	Processing	Dry Matter	Lipid	NDF	ADF	ADL	CP	AP	Ash	TNC
Ritchiea albersii	flower bud		94.0	2.4	16.4	11.8	3.7	34.1	33.0	7.0	41.2
Ritchiea albersii	fruit		94.1	2.6	53.3	38.2	13.4	22.8	20.8	8.6	14.8
Celastraceae											
Hippocratea (Loeseneriella) africana	fruit		92.1	11.5	36.6	27.0	17.4	12.9	10.0	5.2	36.7
Hippocratea (Loeseneriella) africana	mature leaf		93.2	2.8	38.8	25.8	10.2	20.1	17.5	11.1	31.7
Hippocratea (Loeseneriella) africana	stem		95.0	2.0	58.9	45.1	11.7	19.4	16.9	6.8	15.5
Hippocratea (Loeseneriella) africana	young leaf		93.8	2.1	35.0	23.1	5.0	26.9	24.6	10.2	28.0
Hippocratea goetzei	mature leaf		94.1	3.3	35.7	22.5	8.7	28.9	25.7	11.6	23.7
Hippocratea goetzei	stem		95.0	2.8	60.6	51.5	15.9	17.8	15.9	4.7	16.0
Hippocratea goetzei	young leaf		94.8	3.7	30.4	21.7	6.4	29.6	26.3	12.3	27.4
Colchicaceae											
Gloriosa superba	mature leaf		94.5	4.3	28.5	22.0	6.9	27.8	24.8	7.2	35.1
Gloriosa superba	stem		94.9	1.4	60.8	49.5	8.7	8.0	5.8	7.6	24.6
Gloriosa superba	young leaf		93.9	5.4	28.2	24.9	11.7	21.2	17.2	8.6	40.6
Convolvulaceae											
Ipomoea sp.	flower	no petiole	95.0	3.4	26.0	17.7	5.6	15.7	13.0	8.1	49.4
Ipomoea sp.	mature leaf		93.4	3.3	48.6	21.2	7.7	31.8	29.3	11.1	7.6
Ipomoea sp.	stem		94.3	2.2	48.2	38.2	8.9	21.3	19.7	10.5	19.5
Ipomoea sp.	young leaf		93.9	2.6	45.8	29.3	16.0	37.5	34.9	9.6	7.1
Cornaceae											
Alangium chinense	mature leaf	no petiole	93.4	4.3	30.0	18.2	6.0	30.1	27.3	6.3	32.2
Alangium chinense	young leaf	no petiole	94.7	3.8	24.7	18.9	8.1	35.0	33.1	6.0	32.4
Cucurbitaceae											
Cucumis-like sp.	mature leaf	no petiole	93.2	3.4	52.2	29.0	9.9	26.4	21.3	16.6	7.9
Cucumis-like sp.	young leaf		93.6	2.3	50.0	27.1	7.3	30.2	27.4	9.0	12.7
Momordica foetida	fruit		93.1	3.9	30.1	23.2	10.7	18.5	16.9	3.8	45.3
Momordica foetida	mature leaf		93.8	2.7	31.9	21.1	8.1	32.3	26.3	23.1	16.6
Momordica foetida	young leaf		92.9	2.6	21.9	14.5	4.6	34.5	32.4	5.6	37.6
Momordica foetida	young leaf, mature leaf		93.3	4.5	27.7	16.2	6.8	35.1	29.7	13.2	26.9

Scientific name	Part	Processing	Dry Matter	Lipid	NDF	ADF	ADL	CP	AP	Ash	TNC
Momordica-like sp.	mature leaf		93.2	3.2	30.4	21.8	15.5	36.6	32.0	15.9	18.6
Peponium vogelii	flower bud		93.0	3.5	44.8	31.5	15.4	34.5	27.2	14.4	12.1
Cupressaceae											
Cupressus lusitanica	flower	seed cones	92.9	5.1	61.2	55.4	29.0	6.2	2.6	2.9	28.2
Cupressus lusitanica	flower	pollen cones	91.6	2.3	38.7	27.3	19.0	6.2	3.6	3.2	52.2
Ebenaceae											
Diospyros abyssinica	leaf bud		93.6	2.2	21.5	12.9	6.7	35.2	33.8	4.2	38.3
Diospyros abyssinica	mature leaf		94.0	2.9	49.0	29.1	11.4	17.9	16.1	6.1	26.0
Diospyros abyssinica	young leaf		93.4	1.1	39.2	25.2	12.5	25.9	23.7	5.6	30.4
Euphorbiaceae											
Acalypha neptunica	mature leaf		92.9	1.6	41.3	24.5	6.3	26.9	24.3	19.1	14.1
Acalypha neptunica	young leaf		93.6	2.6	35.2	24.0	7.7	38.2	35.4	14.9	12.3
Croton macrostachyus	mature leaf	no petiole	93.4	1.8	38.3	17.5	6.4	27.4	25.5	8.3	26.2
Croton macrostachyus	young leaf	no petiole	93.5	1.7	34.9	19.8	6.5	33.0	31.0	8.7	23.7
Croton megalocarpus	exudate		93.6	2.9	59.6	4.2	3.0	1.4	1.1	8.0	28.3
Croton megalocarpus	fruit		93.3	1.7	42.9	31.3	17.7	23.1	18.0	7.4	30.0
Croton megalocarpus	young leaf		93.7	3.9	42.7	25.4	9.7	37.6	33.3	8.2	12.0
Croton sylvaticus	fruit		93.7	1.7	33.7	20.4	6.7	24.2	20.1	13.2	31.3
Erythrococca sp.	fruit		92.8	18.7	41.9	34.4	14.9	26.4	23.8	4.0	11.5
Erythrococca sp.	mature leaf		93.2	3.1	42.2	21.1	7.0	30.1	27.2	14.7	13.5
Erythrococca sp.	young leaf		96.4	3.9	33.0	22.8	10.3	44.4	39.5	10.6	12.9
Erythrococca sp.	young leaf, mature leaf		94.4	4.3	28.0	28.6	15.1	39.3	34.8	15.1	18.2
Macaranga capensis	flower		91.5	2.9	31.3	23.2	10.8	14.0	10.4	2.7	52.6
Macaranga capensis	fruit		93.7	11.1	21.5	15.0	4.5	15.3	13.7	8.6	45.0
Sapium (Shirakiopsis) ellipticum	fruit		91.8	10.0	36.1	28.6	13.8	18.2	15.2	3.1	35.7
Sapium (Shirakiopsis) ellipticum	leaf bud		93.6	3.0	20.5	15.1	7.6	34.4	29.9	4.7	41.9
Sapium (Shirakiopsis) ellipticum	mature leaf		93.9	3.4	32.5	21.0	8.2	15.7	12.9	7.9	43.3
Sapium (Shirakiopsis) ellipticum	young leaf		93.7	2.4	27.1	17.2	8.4	19.5	17.5	5.2	47.9
Fabaceae											

Scientific name	Part	Processing	Dry Matter	Lipid	NDF	ADF	ADL	CP	AP	Ash	TNC
Calliandra gilberti	mature leaf		92.9	1.4	45.6	27.5	13.3	26.1	20.1	4.8	28.1
Calliandra gilberti	young leaf		90.8	2.4	32.7	20.6	10.6	34.4	28.4	3.3	33.1
Fabaceae – Caesalpinioideae											
Acrocarpus fraxinifolius	flower		93.7	1.5	30.7	23.0	9.1	17.7	15.0	5.6	47.2
Acrocarpus fraxinifolius	fruit		93.4	3.1	21.3	13.7	3.0	26.3	25.3	4.0	46.3
Acrocarpus fraxinifolius	leaf bud, young leaf		94.2	2.0	26.3	20.6	13.6	25.2	20.2	3.9	47.6
Acrocarpus fraxinifolius	young leaf		93.6	1.5	22.1	17.8	8.9	21.6	18.0	2.6	55.9
Fabaceae – Mimosoideae											
Acacia abyssinica	bark		90.3	2.4	78.7	69.2	46.9	6.5	2.3	7.1	9.6
Acacia abyssinica	exudate		91.9	2.0	37.9	1.9	1.5	2.2	1.9	1.5	56.8
Acacia abyssinica	flower bud, flower		92.2	3.1	37.8	30.7	19.6	15.8	10.6	3.4	45.2
Acacia abyssinica	leaf bud, young leaf		92.5	2.5	38.7	18.5	10.5	32.8	29.2	6.3	23.2
Albizia gummifera	exudate		90.4	1.9	43.2	11.9	6.1	8.2	6.8	12.2	35.9
Albizia gummifera	leaf bud, young leaf		93.1	2.5	50.6	38.4	23.0	40.4	33.0	3.2	10.7
Albizia gummifera	mature leaf		93.4	0.5	62.6	47.9	31.9	23.7	15.0	5.2	16.7
Albizia gummifera	young leaf		93.5	2.1	42.6	25.0	16.5	45.2	41.5	1.0	12.8
Fabaceae – Papilionoideae											
Vigna sp.	mature leaf		93.5	2.6	54.3	29.0	9.3	29.5	27.1	7.6	8.3
Vigna sp.	young leaf		93.8	3.1	43.2	24.6	7.9	35.4	33.3	10.2	11.0
Hypericaceae											
Harungana madagascariensis	flower bud		93.7	2.3	40.4	33.1	17.7	17.4	11.4	6.1	39.8
Harungana madagascariensis	fruit		94.5	7.3	30.1	26.3	14.5	6.0	4.0	4.6	54.0
Harungana madagascariensis	leaf bud		91.5	2.8	54.1	49.3	28.8	13.7	7.4	2.9	32.8
Harungana madagascariensis	mature leaf		92.6	1.7	40.6	30.9	15.3	14.9	10.3	6.5	40.8
Harungana madagascariensis	stem		94.8	0.7	69.1	55.7	17.3	5.9	3.2	2.3	24.6
Harungana madagascariensis	young leaf		92.3	3.6	40.7	31.6	17.0	16.0	10.7	2.7	42.2
Lamiaceae											
Clerodendrum silvanum	mature leaf		94.5	3.2	59.1	37.4	20.2	24.0	17.1	3.8	16.7
Clerodendrum silvanum	young leaf		94.5	1.6	43.0	25.1	12.5	38.1	32.2	6.5	16.8

Scientific name	Part	Processing	Dry Matter	Lipid	NDF	ADF	ADL	CP	AP	Ash	TNC
Vitex doniana	leaf bud		94.3	3.2	45.2	37.2	24.2	24.8	15.2	10.2	26.9
Vitex doniana	leaf bud, young leaf		93.8	3.4	50.1	41.9	27.1	29.3	16.1	8.4	22.1
Vitex doniana	mature leaf		93.3	2.1	53.2	41.5	23.8	23.7	12.9	8.1	23.7
Vitex doniana	stem		93.4	2.1	66.8	53.2	21.2	7.3	3.1	1.1	27.0
Lauraceae											
Persea americana, avocado	flower bud, flower		94.4	3.8	34.1	22.8	9.4	20.2	16.2	4.6	41.3
Persea americana, avocado	stem		93.6	1.7	51.5	39.9	17.3	6.5	3.4	5.0	38.4
Leguminosae-Papilionaceae											
Amphicarpa africana	mature leaf		94.0	3.6	49.0	28.4	9.5	20.8	17.9	13.1	17.1
Amphicarpa africana	young leaf		91.9	4.0	46.4	28.3	13.8	38.7	35.1	11.0	3.5
Meliaceae											
Khaya anthotheca	exudate		89.2	1.7	58.2	2.1	1.7	6.5	6.5	11.0	22.6
Khaya anthotheca	stem		94.4	1.5	72.7	58.7	15.3	9.2	6.9	1.8	17.2
Lepidotrichilia volkensii	fruit		93.7	2.7	32.7	24.4	12.4	24.6	20.7	9.3	34.6
Lepidotrichilia volkensii	young leaf		94.9	2.7	35.2	26.5	13.9	36.2	30.2	7.5	24.4
Lepidotrichilia volkensii	young leaf, mature leaf		94.6	3.5	42.9	25.7	12.3	25.9	21.7	13.1	19.0
Trichilia emetica	leaf bud		93.4	4.3	40.9	35.7	24.6	28.4	21.4	5.3	28.1
Trichilia emetica	mature leaf	no petiole	93.2	9.6	48.3	36.5	17.7	13.2	11.0	6.7	24.4
Trichilia emetica	young leaf	no petiole	93.7	4.5	42.5	30.5	18.4	28.4	25.3	10.0	20.3
Turraea holstii	leaf bud		94.5	4.9	27.4	21.2	9.5	31.1	27.5	9.0	31.1
Turraea holstii	mature leaf		94.2	6.2	32.3	22.9	11.6	21.8	20.0	13.3	29.6
Turraea holstii	young leaf		94.9	7.1	34.6	28.5	17.1	21.2	19.5	7.9	30.9
Melianthaceae											
Bersama abysinnica	young leaf, mature leaf		92.2	2.6	40.6	27.2	7.0	15.6	11.8	11.7	33.2
Menispermaceae											
Tiliacoria sp. (kenyensis, funifera)	flower bud, flower		92.7	2.2	46.2	29.0	13.9	32.1	27.9	5.4	18.3
Tiliacoria sp. (kenyensis, funifera)	stem		93.7	0.7	74.0	55.3	18.9	17.9	13.8	4.0	7.5
Tiliacoria sp. (kenyensis, funifera)	young leaf		93.5	0.9	59.2	38.3	18.5	35.5	28.7	4.3	6.8
Moraceae											

Scientific name	Part	Processing	Dry Matter	Lipid	NDF	ADF	ADL	CP	AP	Ash	TNC
Antiaris toxicaria	flower bud, flower		92.6	2.8	60.0	50.2	31.7	20.4	11.6	10.4	16.2
Antiaris toxicaria	leaf bud		92.9	2.7	46.9	35.3	14.8	28.1	20.3	8.7	21.3
Antiaris toxicaria	ripe fruit		93.5	8.7	20.2	16.3	6.8	19.0	17.2	9.1	44.7
Antiaris toxicaria	stem		94.1	1.6	64.5	50.2	13.0	15.2	12.5	9.5	11.9
Antiaris toxicaria	young leaf		92.9	1.7	44.0	29.6	15.5	21.3	17.2	6.5	30.7
Ficus asperifolia	fruit		93.1	11.7	27.9	22.5	5.8	21.6	20.2	9.2	31.0
Ficus cyathistipula	young leaf		92.6	2.6	53.3	40.1	17.3	13.6	11.3	7.7	25.1
Ficus exasperata	fruit		93.1	10.7	38.3	29.2	12.5	21.1	18.0	9.6	23.4
Ficus exasperata	leaf bud		93.8	2.8	32.8	21.3	6.6	41.4	39.2	12.6	12.6
Ficus exasperata	young leaf		93.6	2.4	33.2	25.2	12.5	34.7	29.7	12.5	23.7
Ficus lutea	fruit		92.2	2.5	58.9	45.5	25.7	10.5	6.3	7.8	24.5
Ficus lutea	leaf bud		91.6	4.1	59.1	55.5	39.4	18.3	9.1	7.8	19.9
Ficus lutea	young leaf		91.7	2.3	56.5	52.0	38.2	18.5	9.9	5.5	25.8
Ficus ovata	young leaf		92.2	3.4	52.7	41.7	26.7	16.0	10.5	11.7	21.7
Ficus sansibarica (brachylepis, chirindensis)	fruit		91.3	4.3	47.1	39.3	19.5	8.7	5.1	5.3	38.2
Ficus sansibarica (brachylepis, chirindensis)	leaf bud		92.7	2.5	33.8	25.2	13.6	22.7	17.8	8.8	37.1
Ficus sansibarica (brachylepis, chirindensis)	ripe fruit		93.4	4.4	28.5	23.5	8.2	12.7	11.1	10.8	45.3
Ficus sansibarica (brachylepis, chirindensis)	young leaf		92.9	2.4	31.9	20.1	8.1	21.2	18.5	9.1	38.5
Ficus sur (capensis, mallatocarpa)	fruit		88.8	3.7	34.4	33.2	19.4	6.4	2.5	8.3	51.1
Ficus sur (capensis, mallatocarpa)	leaf bud		93.0	2.7	40.0	32.6	16.3	26.3	20.2	10.6	26.5
Ficus sur (capensis, mallatocarpa)	young leaf		92.5	2.5	42.3	36.0	25.3	29.1	23.4	9.6	24.5
Ficus thonningii	fruit		93.6	4.0	65.0	54.2	25.2	6.1	2.0	4.5	24.4
Ficus thonningii	leaf bud		92.4	3.6	50.2	37.9	22.5	18.1	12.7	10.8	22.7
Ficus thonningii	young leaf		92.7	2.0	54.8	39.4	20.9	16.2	9.8	13.1	20.3
Morus lactea (mesozygia)	fruit		93.4	4.1	23.4	19.4	12.6	16.6	14.6	6.8	51.1
Morus lactea (mesozygia)	leaf bud		94.0	2.7	22.3	15.9	4.8	39.0	36.7	7.3	31.0
Morus lactea (mesozygia)	mature leaf		93.4	3.7	42.9	23.3	11.8	25.7	23.9	9.3	20.2
Morus lactea (mesozygia)	young leaf		92.4	1.4	38.7	26.0	14.2	33.6	27.2	8.6	24.0

Scientific name	Part	Processing	Dry Matter	Lipid	NDF	ADF	ADL	CP	AP	Ash	TNC
Trilepisium madagascariense (Bosqueia phoberos)	leaf bud		93.4	2.6	35.5	24.0	9.6	28.3	24.9	9.5	27.5
Trilepisium madagascariense (Bosqueia phoberos)	mature leaf		93.3	4.6	50.3	26.3	9.6	16.8	13.1	11.8	21.5
Trilepisium madagascariense (Bosqueia phoberos)	young leaf		93.5	4.2	55.4	28.1	12.7	19.0	14.7	9.9	15.8
Myrsinaceae											
Maesa lanceolata	mature leaf		93.0	7.0	37.0	30.8	19.6	23.2	17.5	7.4	31.1
Myrtaceae											
Callistemon citrinus, bottlebrush	flower		94.8	5.8	27.5	19.3	6.3	6.9	5.7	4.1	56.9
Eucalyptus saligna	bark		90.3	1.6	74.7	64.1	30.8	5.6	0.8	9.0	13.9
Eucalyptus saligna	exudate		88.7	0.7	1.8	0.9	0.7	0.6	0.6	1.3	95.7
Eucalyptus saligna	fruit	seeds only	92.9	7.2	85.3	78.0	35.7	8.0	4.9	<0.1	4.0
Eucalyptus saligna	fruit	no seeds	93.1	4.8	60.1	46.9	18.5	5.2	2.2	4.2	28.7
Psidium guajava	fruit		92.7	10.7	40.9	34.0	12.7	11.9	10.4	3.1	34.9
Psidium guajava	ripe fruit		94.6	6.7	53.6	45.3	19.2	7.9	5.4	7.0	27.4
Oleaceae											
Jasmimum abyssinica	mature leaf		94.1	3.1	53.9	34.7	21.9	20.6	11.6	5.3	26.1
Jasmimum abyssinica	young leaf		93.7	2.2	48.9	31.0	20.6	25.2	15.3	3.7	29.8
Jasmimum pauciflorum	mature leaf		93.9	2.4	56.3	28.9	14.7	24.1	18.5	9.3	14.0
Jasmimum pauciflorum	young leaf		94.4	3.1	57.3	29.7	15.8	21.5	14.9	10.4	14.9
Olea capensis (welwitschii)	fruit		91.2	2.0	73.6	59.2	25.4	6.3	1.9	1.6	20.9
Olea capensis (welwitschii)	leaf bud		94.9	6.5	44.9	31.1	24.1	20.1	8.2	3.4	37.0
Olea capensis (welwitschii)	mature leaf		94.7	5.1	37.9	28.1	17.9	10.6	3.9	4.0	49.1
Olea capensis (welwitschii)	young leaf		95.4	9.5	46.7	34.2	25.5	21.0	8.6	5.3	29.8
Orchidaceae											
orchid morphotype	young leaf, mature leaf		92.5	4.8	49.8	32.0	12.7	13.8	9.3	12.6	26.6
Passifloraceae											
Adenia bequaertii	ripe fruit		no seed	95.2	2.3	21.7	19.7	7.2	7.2	5.1	13.3

Scientific name	Part	Processing	Dry Matter	Lipid	NDF	ADF	ADL	CP	AP	Ash	TNC
Adenia bequaertii	stem		92.4	1.0	45.2	41.1	21.9	12.3	6.4	12.9	35.2
Adenia bequaertii	unripe fruit	no seed	93.3	1.8	30.7	25.7	12.7	7.7	4.6	10.5	52.7
Adenia bequaertii	young leaf		92.4	3.1	41.2	32.3	22.8	27.6	21.4	10.0	24.9
Passiflora sp.	unripe fruit		94.2	3.1	37.6	28.5	6.4	17.1	15.2	2.9	41.2
Passiflora sp.	young leaf		94.2	4.3	23.4	19.1	9.0	34.8	30.0	6.0	36.3
Passiflora sp.	tendril		93.8	1.8	53.2	44.4	13.4	18.3	16.2	8.6	20.1
Phyllanthaceae											
Bischofia javanica	bark		89.3	1.7	78.5	74.8	49.2	4.0	2.3	8.0	9.6
Bischofia javanica	flower		92.5	2.5	30.4	25.9	17.5	18.9	14.1	9.6	43.4
Bischofia javanica	fruit		93.5	6.4	57.4	57.1	29.7	5.8	0.1	4.8	31.2
Bischofia javanica	mature leaf		93.3	2.4	40.4	31.9	15.4	12.7	8.3	9.1	39.8
Bischofia javanica	stem	mature	92.8	1.0	54.6	49.2	16.5	9.5	6.9	8.2	29.2
Bischofia javanica	stem	young	93.9	2.1	41.2	36.8	14.0	12.0	8.9	13.2	35.3
Bischofia javanica	young leaf		92.8	3.2	37.2	31.8	17.6	13.6	9.7	9.6	40.4
Bridelia micrantha	bark		89.2	2.3	79.2	78.4	59.0	9.7	3.2	7.7	7.7
Bridelia micrantha	fruit		92.4	3.7	53.0	43.1	22.8	11.9	8.0	3.3	31.9
Bridelia micrantha	leaf bud		92.2	1.9	40.7	32.2	15.9	20.7	15.3	4.7	37.3
Bridelia micrantha	young leaf		92.9	1.2	41.5	31.2	16.6	18.9	12.4	8.1	36.8
Margaritaria (Phyllanthus) discoidea	mature leaf		94.0	3.5	39.9	19.7	4.1	26.8	25.3	4.4	26.9
Margaritaria (Phyllanthus) discoidea	young leaf		94.4	4.0	35.9	17.6	3.9	25.7	22.4	9.6	28.1
Phyllanthus sp.	young leaf		92.7	3.1	44.4	16.9	4.3	27.8	25.1	4.8	22.6
Phyllanthus sp.	young leaf, mature leaf		93.4	3.2	43.2	17.0	4.5	23.5	19.6	10.5	23.5
Piperaceae											
Piper capense	fruit		93.7	5.4	23.0	17.6	6.9	32.7	30.7	10.6	31.1
Piper capense	leaf bud, young leaf		93.9	4.0	22.1	16.7	4.4	43.2	38.6	11.8	24.9
Piper capense	mature leaf		94.1	4.3	37.9	27.4	14.9	27.6	25.7	10.6	23.8
Piper capense	ripe fruit		92.7	6.5	29.0	23.0	10.2	22.0	18.5	9.0	37.0
Piper capense	stem		94.4	1.5	59.9	48.8	13.5	9.3	7.6	7.0	24.0
Piper capense	unripe fruit		92.8	3.9	23.2	17.1	7.8	25.1	21.9	10.3	40.7

Scientific name	Part	Processing	Dry Matter	Lipid	NDF	ADF	ADL	CP	AP	Ash	TNC
Piper capense	young leaf		94.3	5.6	26.5	20.7	8.3	39.1	36.6	11.5	19.9
Piper guineense	leaf bud		94.8	3.8	30.9	19.5	10.0	40.4	37.2	8.5	19.6
Piper guineense	young leaf		95.1	6.1	31.2	24.1	13.7	24.0	22.6	10.0	30.0
Piper umbellatum	leaf bud		95.2	12.2	25.4	17.1	6.3	34.2	32.0	11.7	19.1
Piper umbellatum	mature leaf		94.2	7.9	31.6	23.5	14.6	26.9	25.1	12.7	22.7
Piper umbellatum	stem		94.3	4.0	39.1	30.7	6.0	16.2	14.0	22.4	20.4
Piper umbellatum	young leaf		94.8	11.2	21.8	15.7	4.8	30.4	28.8	11.6	26.8
Poaceae											
grass	young leaf, mature leaf		94.1	2.9	62.2	28.6	3.6	18.8	16.2	10.0	8.8
ugali		cooked	89.6	2.2	11.9	5.2	1.0	10.3	9.1	<0.1	76.9
Zea sp., maize	kernels		90.0	7.2	12.3	4.1	1.0	9.0	9.0	0.2	71.2
Rhamnaceae											
Maesopsis eminii	ripe fruit		93.4	2.6	30.9	27.3	21.7	12.2	7.3	6.1	53.2
Maesopsis eminii	unripe fruit		91.7	0.8	50.8	47.1	10.2	15.2	7.6	5.4	35.4
Maesopsis eminii	young leaf		92.6	2.7	22.4	15.8	8.4	32.1	28.6	6.7	39.6
Scutia myrtina	young leaf		92.5	1.7	47.9	30.7	18.4	18.8	13.8	7.0	29.6
Rhizophoraceae											
Cassipourea ruwensorensis	leaf bud		93.5	0.3	50.7	32.7	12.2	28.7	25.0	6.9	17.1
Cassipourea ruwensorensis	young leaf		93.2	0.4	51.6	30.3	12.5	24.7	20.6	7.6	19.8
Rosaceae											
Eriobotrya japonica	fruit	no seed	92.7	3.1	27.1	22.4	13.3	6.9	4.5	6.2	59.1
Oxyanthus speciosus	fruit		93.0	1.3	29.8	22.3	10.7	15.3	10.9	7.3	50.6
Prunus africana	bark		89.3	0.5	72.8	65.4	43.2	5.6	<0.1	11.2	16.7
Prunus africana	exudate		96.2	5.1	71.7	4.1	3.3	0.4	0.3	5.2	17.7
Prunus africana	fruit		94.9	1.3	32.5	25.2	13.2	17.9	14.6	5.5	46.1
Prunus africana	young leaf		94.2	3.7	30.2	16.7	7.9	17.4	15.3	7.6	43.2
Rubus rigidus	fruit	no midrib	93.8	12.2	47.4	39.5	17.7	10.9	9.2	5.3	25.8
Rubus rigidus	mature leaf		92.4	3.0	46.1	21.7	5.2	13.5	12.1	6.7	32.1
Rubus rigidus	stem		94.3	0.8	66.5	53.5	12.9	6.8	4.9	6.4	21.5

Scientific name	Part	Processing	Dry Matter	Lipid	NDF	ADF	ADL	CP	AP	Ash	TNC
Rubus rigidus	unripe fruit		91.8	5.3	55.4	45.4	20.9	12.4	10.0	1.9	27.3
Rubus rigidus	young leaf		92.4	2.7	41.0	22.7	6.2	20.7	18.5	6.4	31.4
Rubiaceae											
Aulacocalyx diervilleoides	flower	no petiole	93.8	3.7	31.4	23.4	14.3	19.7	15.3	2.0	47.6
Aulacocalyx diervilleoides	flower bud	no petiole	93.7	4.0	37.5	26.3	16.1	24.9	18.5	5.7	34.2
Aulacocalyx diervilleoides	fruit		95.0	3.3	49.1	39.7	26.0	20.6	9.8	3.4	34.4
Aulacocalyx diervilleoides	leaf bud, young leaf		94.6	2.6	47.3	31.4	20.4	43.5	36.5	7.6	6.0
Aulacocalyx diervilleoides	young leaf		94.7	4.7	46.7	33.2	21.1	37.9	29.8	8.3	12.2
Keetia gueinzii	fruit		92.6	4.2	45.9	37.8	17.2	7.3	3.9	0.8	45.2
Keetia gueinzii	young leaf		92.5	2.0	45.2	29.8	16.2	21.2	16.0	3.6	33.2
Keetia gueinzii	young leaf, mature leaf		93.1	3.0	41.8	23.3	12.2	18.0	14.9	2.4	37.9
Pavetta abyssinica	mature leaf	no petiole	95.8	3.3	29.6	19.4	7.8	18.2	15.4	8.5	43.1
Pavetta abyssinica	young leaf		93.9	1.7	35.4	28.4	19.5	23.6	17.9	5.3	39.7
Pavetta sp.	mature leaf		94.4	2.7	27.7	17.1	5.8	20.2	19.1	7.8	42.7
Pavetta sp.	young leaf		95.6	2.3	33.6	24.0	13.4	21.9	15.6	9.4	39.1
Rothmannia urcelliformis	fruit	no seeds	94.0	3.5	53.6	44.3	29.1	24.8	14.5	7.8	20.6
Rothmannia urcelliformis	fruit	with seeds	90.0	2.7	61.8	33.8	4.8	12.8	10.3	0.7	24.6
Rothmannia urcelliformis	mature leaf		93.3	2.2	48.7	33.2	20.3	24.3	17.3	4.9	27.0
Vangueria sp.	fruit		90.7	1.0	34.6	29.7	16.0	12.7	8.9	1.3	54.2
Vangueria sp.	mature leaf	no petiole	94.4	2.5	36.8	26.0	17.4	22.3	15.3	9.4	36.0
Vangueria sp.	young leaf	no petiole	93.7	3.5	47.1	27.3	17.1	24.6	20.0	5.7	23.8
Rutaceae											
Teclea (Vepris) nobilis	leaf bud		93.9	1.7	26.1	16.4	4.2	37.5	36.2	5.9	30.1
Teclea (Vepris) nobilis	young leaf		94.6	1.7	28.5	15.8	5.7	33.4	30.6	5.6	33.7
Zanthoxylum gilletii	bark		91.3	1.4	71.4	60.2	30.6	7.9	5.8	3.3	18.0
Zanthoxylum gilletii	exudate		92.9	1.4	2.3	0.7	0.4	1.4	1.4	4.0	91.0
Zanthoxylum gilletii	flower bud, flower		91.9	1.9	41.5	32.7	13.9	22.2	17.6	7.3	31.6
Zanthoxylum gilletii	fruit		95.7	38.9	39.7	41.2	41.0	13.9	12.9	6.4	4.6
Zanthoxylum gilletii	leaf bud		93.4	1.3	27.5	19.3	5.4	28.9	26.3	4.7	40.2

Scientific name	Part	Processing	Dry Matter	Lipid	NDF	ADF	ADL	CP	AP	Ash	TNC
Zanthoxylum gilletii	stem		93.5	0.7	43.9	33.2	8.3	14.7	8.7	7.2	39.5
Zanthoxylum gilletii	unripe fruit		93.6	2.4	56.1	46.0	20.4	12.4	9.5	3.2	28.7
Zanthoxylum gilletii	young leaf		93.5	1.9	27.5	20.0	5.6	31.9	29.7	4.4	36.5
Zanthoxylum mildbraedii	flower		92.9	3.5	51.3	47.6	32.6	25.3	17.6	8.2	19.3
Zanthoxylum mildbraedii	leaf bud		93.3	2.2	33.7	27.0	14.0	26.3	23.3	6.9	33.9
Zanthoxylum mildbraedii	young leaf		93.5	2.6	29.6	22.0	13.5	36.0	32.7	7.9	27.2
Salicaceae											
Casearia battiscombei	fruit		96.5	34.1	23.6	17.9	5.0	10.5	9.5	19.3	13.4
Casearia battiscombei	mature leaf		92.7	4.9	36.8	25.3	10.4	13.2	10.7	8.2	39.4
Casearia battiscombei	young leaf		92.7	2.5	36.6	29.0	17.4	20.5	16.4	6.1	38.6
Dovyalis macrocalyx	fruit		95.2	7.1	17.5	10.9	2.3	31.3	30.3	11.2	35.7
Dovyalis macrocalyx	mature leaf	no petiole	93.8	3.4	45.4	24.3	8.6	20.9	19.1	12.8	19.2
Dovyalis macrocalyx	ripe fruit		94.9	6.9	14.3	10.1	3.5	15.4	15.3	5.5	58.0
Dovyalis macrocalyx	unripe fruit		95.0	7.9	25.3	18.5	6.7	25.2	23.5	9.5	33.8
Dovyalis macrocalyx	young leaf	no petiole	93.1	1.3	36.3	19.4	7.6	30.3	28.2	9.9	24.3
Dovyalis macrocalyx	young leaf, mature leaf	no petiole	93.5	3.3	44.0	24.0	9.2	25.5	23.9	11.9	17.0
Sapindaceae											
Blighia unijugata	young leaf		94.5	1.8	42.6	30.5	13.7	24.3	18.6	7.3	29.8
Sapotaceae											
Aningeria (Pouteria) altissima	flower bud, flower		92.7	3.6	61.2	44.0	26.4	15.0	8.5	4.3	22.4
Aningeria (Pouteria) altissima	fruit		93.5	12.1	44.1	39.4	24.0	23.6	14.9	17.9	12.5
Aningeria (Pouteria) altissima	leaf bud		93.1	3.5	49.8	38.6	21.2	27.2	21.9	5.3	19.5
Aningeria (Pouteria) altissima	stem		93.7	1.1	77.5	64.6	22.2	7.3	4.2	1.5	15.7
Aningeria (Pouteria) altissima	young leaf		93.1	4.4	53.6	38.1	21.3	15.7	15.2	3.6	23.2
Bequaertiodendron oblanceolatum	fruit		94.5	4.3	41.3	29.4	17.5	11.9	7.3	7.0	40.2
Bequaertiodendron oblanceolatum	leaf bud		94.2	4.4	51.9	37.9	13.7	20.8	16.7	8.1	18.9
Bequaertiodendron oblanceolatum	unripe fruit		93.5	3.1	39.5	24.5	14.5	15.8	14.6	3.3	39.5
Bequaertiodendron oblanceolatum	young leaf		94.8	4.7	58.7	41.9	17.6	17.4	12.6	8.8	15.1
Manilkara butugi	fruit		91.3	1.3	75.2	68.3	45.7	11.8	4.1	1.7	17.7

Scientific name	Part	Processing	Dry Matter	Lipid	NDF	ADF	ADL	CP	AP	Ash	TNC
Manilkara butugi	leaf bud		93.2	2.0	45.8	32.2	12.8	21.0	17.7	5.4	29.0
Manilkara butugi	mature leaf		92.2	4.5	47.1	36.2	18.8	13.8	8.9	5.2	34.3
Manilkara butugi	young leaf		93.1	1.9	49.8	41.1	25.0	15.6	9.1	5.5	33.6
Smilacaceae											
Smilax anceps	mature leaf		93.0	2.1	57.7	30.2	14.9	22.5	19.3	5.3	15.6
Smilax anceps	young leaf		91.6	3.0	37.2	28.6	19.2	17.2	11.4	4.8	43.7
Smilax anceps	young leaf, mature leaf		94.5	4.9	51.4	31.7	11.8	18.4	13.7	6.6	23.4
Solanaceae											
Brunfelsia pauciflora	flower		95.2	3.3	21.1	14.3	6.5	19.5	17.6	3.6	54.4
Solanum mauritianum	fruit		93.0	9.5	45.1	37.3	18.6	15.2	12.7	18.7	14.6
Solanum mauritianum	ripe fruit		93.2	11.5	29.3	23.5	11.4	10.6	10.6	22.2	26.4
Solanum mauritianum	stem		94.5	1.0	66.8	52.2	10.1	16.0	14.0	9.2	9.0
Solanum terminale	mature leaf	no petiole	92.8	2.2	49.8	17.4	6.0	30.8	27.8	12.8	7.4
Solanum terminale	young leaf	no petiole	93.5	1.3	48.0	19.6	6.1	37.8	34.1	10.6	7.3
Ulmaceae											
Chaetacme aristata	leaf bud		93.2	2.3	47.2	24.8	13.6	37.1	31.8	7.5	11.2
Chaetacme aristata	mature leaf		92.1	0.8	55.3	31.8	11.8	18.0	15.6	17.2	13.9
Chaetacme aristata	young leaf		92.8	2.1	48.7	25.2	8.2	27.4	24.3	13.2	13.5
Urticaceae											
Urera trinervis	flower		94.2	2.4	34.3	26.6	16.6	27.9	23.2	24.6	20.8
Urera trinervis	fruit		93.5	8.0	38.4	29.2	14.6	27.7	23.3	18.7	12.8
Urera trinervis	leaf bud		91.7	1.8	40.4	28.4	16.9	26.5	20.2	17.3	21.8
Urera trinervis	stem		92.6	2.2	44.2	32.6	12.4	21.8	18.1	20.7	15.1
Urera trinervis	young leaf		91.4	1.8	40.4	27.3	15.9	25.2	19.1	15.7	25.5
Verbenaceae											
Lantana camara	flower		93.3	2.8	34.7	28.3	16.9	18.6	13.5	6.9	42.1
Lantana camara	flower bud		92.4	2.0	43.2	34.9	20.1	24.1	15.6	7.2	32.0
Lantana camara	fruit		93.4	1.1	62.6	51.4	23.2	6.2	3.3	3.6	29.4
Lantana camara	leaf bud, young leaf		93.1	3.0	37.7	28.3	15.1	27.3	20.5	5.3	33.5

Scientific name	Part	Processing	Dry Matter	Lipid	NDF	ADF	ADL	CP	AP	Ash	TNC
Lantana camara	mature leaf		93.3	3.0	42.2	29.5	18.9	30.5	23.9	10.0	21.0
Lantana camara	young leaf		93.0	4.2	35.0	26.3	16.0	18.1	10.7	8.0	42.1
Zingiberaceae											
Aframomum sp.	fruit		94.0	1.1	38.2	24.4	1.8	5.4	4.3	5.8	50.7
Aframomum sp.	stem	young	94.3	1.6	73.4	53.9	12.6	10.1	6.9	12.2	7.7
Mushroom morphotypes											
general			91.2	2.6	60.3	38.5	1.9	<0.1	15.7	8.4	13.1
orange-colored			93.1	2.5	59.8	37.6	2.5	17.7	13.1	13.4	12.4
white trumpet-shaped			88.8	1.2	80.4	53.5	0.9	12.5	10.1	3.9	4.7
woodears			88.3	1.0	49.1	28.5	3.3	15.2	12.3	8.6	29.0
Insect morphotypes											
cricket			90.8	16.4		26.1			37.8	4.3	15.4
grasshopper			90.5	10.5		15.3			38.4	3.3	32.6
hairy caterpillar			89.8	13.0		18.6			33.6	6.5	28.4
not hairy caterpillar			89.4	28.6		15.9			34.2	6.6	14.7
siafu ants (*Dorylus* spp.)			90.3	9.6		38.9			38.2	7.9	5.3
small black ants			90.5	24.1		31.0			35.9	17.4	1.0
small insects in white residue			95.2	28.2		29.6			15.7	23.0	3.5

Appendix II. Food items that were not collected in this study. In total, they accounted for 2.4% of feeding time (calculated by dividing time females spent feeding on uncollected food items by 988 total hours of feeding observations during study period (N=24 subjects, 371 full day focal follows)). Food items listed alphabetically by family. FL, FB=flower and flower bud. FR=fruit (ripe and unripe fruit and seeds). LB=leaf bud. YL=young leaf. ML=mature leaf. EX=exudate (e.g. sap, gum). ST & WD=stem and wood (including bark, petiole, pith, and tendrils).

Plant species/morphotype	part	% of time feeding
Acanthaceae		
Brillantaisia sp.	ML	<0.01
Mimulopsis solmsii	LB	<0.01
Thunbergia alata	ML	0.09
Amaranthaceae		
Achyranthes aspera	YL & ML	<0.01
Cyathula sp.	LB	<0.01
Cyathula sp.	ST & WD	<0.01
Apocynaceae		
Funtumia africana (latifolia)	LB	0.01
Mondia whitei	ML	<0.01
Mondia whitei	YL	<0.01
Tabernaemontana usambarensis (ventricosa)	ML	<0.01
Asteraceae		
Bidens formosa	YL	<0.01
Vernonia sp.	YL & ML	0.03
Balsaminaceae		
Impatiens sp.	FL, FB	0.01
Bignoniaceae		
Kigelia africana	FL, FB	<0.01
Markhamia lutea (platycalyx)	FR	<0.01
Markhamia lutea (platycalyx)	LB	<0.01
Spathodea campanulata (nilotica)	YL & ML	0.01
Boraginaceae		
Ehretia cymosa	LB	<0.01
Ehretia cymosa	ML	0.01
Cannabaceae		
Celtis africana	FL, FB	0.14
Celtis africana	ST & WD	<0.01
Celastraceae		
Hippocratea (Loeseneriella) africana	LB	<0.01

Plant species/morphotype	part	% of time feeding
Hippocratea goetzei	LB	<0.01
Mayterius heterophylla	YL	<0.01
Cornaceae		
Alangium chinense	ST & WD	<0.01
Cucurbitaceae		
Momordica sp.	FR	0.01
Peponium vogelii	ML	<0.01
Peponium vogelii	ST & WD	<0.01
Peponium vogelii	YL	<0.01
Cupressaceae		
Cupressus lusitanica	EX	<0.01
Ebenaceae		
Diospyros abyssinica	FL, FB	0.05
Euphorbiaceae		
Acalypha neptunica	FR	<0.01
Croton macrostachyus	FL, FB	0.18
Croton macrostachyus	FR	0.01
Croton megalocarpus	FL, FB	<0.01
Croton megalocarpus	LB	0.01
Croton sylvaticus	FL, FB	0.01
Cucumis sp.	FL, FB	<0.01
Cucumis sp.	LB	<0.01
Cucumis sp.	ST & WD	0.01
Erythrococca sp.	LB	<0.01
Macaranga capensis	ST & WD	<0.01
Fabaceae – Caesalpinioideae		
Acrocarpus fraxinifolius	ST & WD	0.01
Fabaceae – Mimosoideae		
Acacia abyssinica	YL & ML	<0.01
Albizia gummifera	ST & WD	0.06
Hypericaceae		
Harungana madagascariensis	EX	<0.01
Lamiaceae		
Clerodendrum silvanum	ST & WD	<0.01
Cordia africana (abyssinica)	FL, FB	<0.01
Vitex doniana	YL	0.10
Lauraceae		
Persea americana	FR	0.09
Meliaceae		
Lepidotrichilia volkensii	LB	<0.01
Turraea holstii	FR	<0.01
Menispermaceae		

Plant species/morphotype	part	% of time feeding
Tiliacoria sp. (kenyensis and funifera)	FR	<0.01
Tiliacoria sp. (kenyensis and funifera)	LB	<0.01
Moraceae		
Ficus asperifolia	YL	<0.01
Ficus cyathistipula	LB	0.01
Ficus exasperata	ML	0.05
Ficus exasperata	ST & WD	0.01
Ficus natalensis	FR	0.01
Ficus sansibarica (brachylepis, chirindensis)	EX	0.01
Ficus sur (capensis, mallatocarpa)	YL & ML	<0.01
Ficus thonningii	ST & WD	<0.01
Morus lactea (mesozygia)	FL, FB	0.03
Trilepisium madagascariense (Bosqueia phoberos)	EX	<0.01
Trilepisium madagascariense (Bosqueia phoberos)	FR	0.10
Trilepisium madagascariense (Bosqueia phoberos)	ST & WD	<0.01
Myrtaceae		
Psidium guajava	YL	<0.01
Olacaceae		
Strombosia scheffleri	FL, FB	<0.01
Oleaceae		
Jasmimum abysinica	FL, FB	<0.01
Jasmimum pauciflorum	LB	<0.01
Olea capensis (welwitschii)	EX	<0.01
Olea capensis (welwitschii)	ST & WD	<0.01
Orchidaceae		
unidentified orchid	FL, FB	<0.01
Passifloraceae		
Adenia bequaertii	ML	0.01
Passiflora sp.	FL, FB	<0.01
Passiflora sp.	ML	0.01
Phyllanthaceae		
Margaritaria (Phyllanthus) discoidea	FR	0.09
Phyllanthus sp.	ST & WD	<0.01
Piperaceae		
Piper guineense	FR	<0.01
Piper guineense	ML	0.01
Piper guineense	ST & WD	<0.01
Rhamnaceae		
Maesopsis eminii	FL, FB	0.02
Scutia myrtina	YL	0.01
Rosaceae		
Eriobotrya japonica	LB	<0.01

Plant species/morphotype	part	% of time feeding
Prunus africana	FL, FB	0.01
Prunus africana	ML	0.01
Rubus rigidus	FL, FB	<0.01
Rubus rigidus	LB	<0.01
Rubiaceae		
Aulacocalyx diervilleoides	ML	0.50
Aulacocalyx diervilleoides	ST & WD	<0.01
Keetia gueinzii	ST & WD	0.01
Psychotria sp.	YL & ML	<0.01
Rothmannia urcelliformis	FL, FB	0.02
Rothmannia urcelliformis	LB	<0.01
Rothmannia urcelliformis	YL	0.29
Vangueria sp.	ST & WD	<0.01
Rutaceae		
Teclea (Vepris) nobilis	FL, FB	<0.01
Teclea (Vepris) nobilis	ML	0.04
Teclea (Vepris) nobilis	ST & WD	<0.01
Toddalia asiatica	FR	0.01
Toddalia asiatica	ST & WD	<0.01
Toddalia asiatica	YL	<0.01
Salicaceae		
Casearia battiscombei	FL, FB	0.02
Casearia battiscombei	LB	<0.01
Casearia battiscombei	ST & WD	<0.01
Dovyalis macrocalyx	FL, FB	<0.01
Dovyalis macrocalyx	LB	<0.01
Sapindaceae		
Blighia unijugata	LB	0.02
Blighia unijugata	ST & WD	0.01
Ulmaceae		
Chaetacme aristata	ST & WD	0.01
Urticaceae		
Urera trinervis	YL & ML	<0.01
Verbenaceae		
Lantana camara	ST & WD	<0.01

Appendix III. Food items consumed, represented as percentage of feeding time (calculated by dividing total time females spent feeding upon species/morphotype by 988 total hours of feeding observations during study period (N=24 subjects, 371 full day focal follows)). Common name was used when scientific name was not available or to add clarity. *=Plant species (but not necessarily plant parts) also documented in blue monkey diet in 1987 [Cords, 1987]. ( )=species synonyms [Fischer et al., 2010]. UID=unidentified. FL, FB=flower and flower bud. FR=fruit (ripe and unripe fruit and seeds). LB=leaf bud. YL=young leaf. ML=mature leaf. EX=exudate (e.g. sap, gum). ST & WD=stem and wood (including bark, petiole, pith, and tendrils). [a]=plant part consumed was not unidentified. Fungi (mushroom) morphotypes were not included in list (only mushrooms in general), though observed morphotypes of mushroom consumed in 2015 were the following: "white trumpet-shaped", "small orange", "wood-ear", and "general." Insect morphotypes were not included in list (only insects in general), though observed morphotypes included *siafu* (*Dorylus* spp.), other ants, caterpillars, grasshopper, crickets, cicadas, spiders.

Species/morphotype	Plant parts consumed									% of time feeding
	FL, FB	FR	LB	YL	YL & ML	ML	EX	ST & WD	UID	
* *Bischofia javanica*	0.08	9.87		0.07		0.01		0.27		10.29
Psidium guajava		5.36		<0.01						5.36
Cupressus lusitanica	5.03	<0.01					<0.01			5.03
insect									4.98	4.98
* *Trilepisium madagascariense (Bosqueia phoberos)*		0.10	1.49	2.74	0.03	<0.01	<0.01	<0.01	0.01	4.38
* *Celtis africana*	0.14	0.48	0.55	2.40	0.04	0.01		<0.01	0.06	3.70
* *Erythrococca sp.*		0.14	<0.01	0.51	2.85	0.11			<0.01	3.61
* *Funtumia africana (latifolia)*	0.15	3.42	0.01	<0.01				<0.01	0.02	3.60
* *Ficus exasperata*		1.24	0.53	1.46	0.05	0.03		0.01		3.33
* *Mimulopsis solmsii*			<0.01	0.53	2.47	0.19		<0.01		3.20

Species/morphotype	Plant parts consumed									% of time feeding
	FL, FB	FR	LB	YL	YL & ML	ML	EX	ST & WD	UID	
* *Harungana madagascariensis*	0.27	2.81	<0.01	0.04		0.03	<0.01	<0.01		3.15
* *Aulacocalyx diervilleoides*	0.01	0.06	0.03	1.69	0.97	0.01		<0.01	<0.01	2.77
* *Solanum mauritianum*		1.76						0.89	0.01	2.66
Maesopsis eminii	0.02	2.32		0.09						2.43
Lantana camara	0.18	0.40	<0.01	0.50	1.30	0.04		<0.01		2.42
* *Ficus thonningii*		0.74	0.23	1.37				<0.01		2.34
* *Acacia abyssinica*	0.29		0.42	1.28	0.01		0.22	<0.01	<0.01	2.21
* *Zanthoxylum gilletii*	0.70	0.09	0.01	0.68			0.58	0.04	0.01	2.11
* *Dovyalis macrocalyx*	<0.01	0.27	<0.01	0.65	0.70	0.15			0.02	1.80
* *Morus lactea (mesozygia)*	0.03	1.35	0.02	0.26		0.02				1.68
* *Antiaris toxicaria*	0.04	0.48	0.48	0.48				0.01	0.03	1.52
* *Aningeria (Pouteria) altissima*	0.17	0.73	0.03	0.45				<0.01	0.03	1.41
* *Chaetacme aristata*			0.11	1.14	0.05	0.01		0.01	<0.01	1.33
* *Prunus africana*	0.01	0.22		0.43		0.01	0.37	0.20	<0.01	1.23
* *Olea capensis (welwitschii)*		0.16	0.01	0.97	0.04	0.03	<0.01	<0.01	<0.01	1.22
* *Blighia unijugata*			0.02	0.98	<0.01			0.01		1.01
* *Spathodea campanulata (nilotica)*	0.02	0.01	0.04	0.91	0.01			0.01		1.00
* *Ficus sansibarica (brachylepis, chirindensis)*		0.73	0.07	0.09			0.01			0.90
Dracaena fragrans	0.01	0.83		0.02				0.03		0.89
* *Albizia gummifera*			0.02	0.65	0.10	0.02	0.03	0.06	<0.01	0.87
Polyscias fulva	0.03	<0.01	0.10	0.10			0.62	0.02	<0.01	0.86
* *Teclea (Vepris) nobilis*	<0.01		0.01	0.72	<0.01	0.04		<0.01	<0.01	0.78
Cyathula sp.			<0.01	0.35	0.33	0.05		<0.01	<0.01	0.73
* *Ficus sur (capensis, mallatocarpa)*		0.28	0.07	0.36	0.01					0.72
* *Rothmannia urcelliformis*	0.02	0.03	<0.01	0.14	0.29	0.18			0.01	0.67
Rubus rigidus	<0.01	0.10	<0.01	0.41	0.15	<0.01		0.01		0.67
* *Tiliacoria sp. (kenyensis and funifera)*		<0.01	<0.01	0.51	0.01	0.04		0.07	0.02	0.66
* *Alangium chinense*				0.14	0.40	0.11		<0.01		0.65
soil and dirt									0.61	0.61

Species/morphotype	Plant parts consumed									% of time feeding
	FL, FB	FR	LB	YL	YL & ML	ML	EX	ST & WD	UID	
* *Ficus lutea*		0.35	0.24	0.02						0.61
* *Hippocratea goetzei*			<0.01	0.40	0.16	0.01		0.01		0.57
* *Croton megalocarpus*	<0.01	0.52	0.01	0.03			<0.01			0.56
* *Croton macrostachyus*	0.18	0.01		0.05	0.04	0.23				0.51
unidentified		<0.01		0.01		0.01		0.01	0.46	0.49
* *Lepidotrichilia volkensii*		0.01	<0.01	0.09	0.26	0.07			0.03	0.46
* *Casearia battiscombei*	0.02	0.03	<0.01	0.37	0.01	0.02		<0.01		0.45
* *Piper umbellatum*				0.19	0.10	0.02		0.09		0.41
* *Ipomoea sp.*	0.05			0.07	0.26	<0.01		0.02		0.40
* *Persea americana*	0.14	0.09						0.09		0.31
Urera trinervis	0.02		<0.01	0.24	0.01			<0.01		0.28
* *Bequaertiodendron oblanceolatum*		0.23	0.01	0.03						0.27
* *Vangueria*		0.02		0.13	0.07	0.02		<0.01		0.26
* *Margaritaria (Phyllanthus) discoidea*		0.09		0.06	0.02	0.09				0.25
Impatiens sp.	0.01	0.23								0.24
Turraea holstii		<0.01	<0.01	0.15	0.07	<0.01				0.22
Pavetta sp.				0.09	0.11	0.02			<0.01	0.22
* *Acrocarpus fraxinifolius*	0.03	0.16	<0.01	0.01				0.01		0.22
* *Manilkara butugi*		0.19	<0.01	<0.01	<0.01	0.01				0.21
Elaeis sp.		0.20								0.20
* *Bridelia micrantha*		0.15	0.03	0.01				<0.01	<0.01	0.19
Adenia bequaertii		0.06		0.11	0.01	<0.01		<0.01		0.18
Thunbergia alata	<0.01			0.02	0.15	0.01				0.18
water									0.17	0.17
* *Passiflora sp.*	<0.01	0.01		0.13	0.02	<0.01		0.01		0.16
* *Markhamia lutea (platycalyx)*		<0.01	<0.01	0.10				0.06		0.16
* *Trema guineensis (orientalis)*		0.10	<0.01	0.01	0.01	0.02				0.16
* *Zanthoxylum mildbraedii*	0.10		<0.01	0.06						0.16
* *Croton sylvaticus*	0.01	0.14								0.15

Species/morphotype	Plant parts consumed									% of time feeding
	FL, FB	FR	LB	YL	YL & ML	ML	EX	ST & WD	UID	
* *Diospyros abyssinica*	0.05		<0.01	0.08	<0.01	0.01				0.15
Vitex doniana			0.01	0.10	0.01	0.01		0.02	<0.01	0.15
* *Trichilia emetica*			<0.01	0.11	0.03	0.01				0.15
Eucalyptus saligna		0.09					0.02	0.04		0.15
* *Hippocratea (Loeseneriella) africana*		0.07	<0.01	0.02	0.02	0.03		<0.01		0.14
"ugali"									0.13	0.13
Mushroom/fungi sp.									0.12	0.12
Cucumis sp.	<0.01		<0.01	0.02	0.03	0.04		0.01	0.01	0.10
* *Phyllanthus sp.*				0.04	0.04	0.01		<0.01		0.08
* *Ficus cyathistipula*			0.01	0.07						0.08
Solanum terminale				0.03	0.02	0.02				0.07
Bidens formosa	0.02			<0.01				0.03	0.02	0.07
Aframomum sp.		0.01						0.05		0.06
* *Ehretia cymosa*			<0.01	0.05	<0.01	<0.01		<0.01		0.06
* *Celtis durandii*				0.05						0.05
Vernonia sp.					0.05					0.05
* *Kigelia africana*	<0.01			0.05	<0.01					0.05
* *Momordica foetida*		0.02		0.02	0.01	0.01			<0.01	0.05
* *Musa paradisaca*		0.05								0.05
Melanthera scandens				0.01	0.04	<0.01				0.05
* *Piper guineense*		<0.01	<0.01	0.03		0.01		<0.01		0.05
Ficus asperifolia		0.04		<0.01						0.04
* *Piper capense*		0.03	<0.01	<0.01		<0.01		<0.01	<0.01	0.04
* *Brillantaisia sp.*				<0.01		<0.01		0.04		0.04
* *Sapium (Shirakiopsis) ellipticum*		0.01		0.02		<0.01				0.04
Erlangea sp.				0.02	0.01	0.01				0.03
Amphicarpa africana				0.02	<0.01	0.01				0.03
Pavetta abyssinica				0.02	0.01					0.03
* *Khaya anthotheca*							0.03	<0.01		0.03

	Species/morphotype	Plant parts consumed									% of time feeding
		FL, FB	FR	LB	YL	YL & ML	ML	EX	ST & WD	UID	
	"maize"		0.03								0.03
	Eriobotrya japonica		0.02	<0.01							0.02
	Bersama abysinnica				<0.01	0.02					0.02
	Citrus sp., orange		0.02								0.02
	Ipomoea sp., sweet potato									0.02	0.02
	Macaranga capensis		0.01						<0.01	<0.01	0.02
*	*Clerodendrum silvanum*				0.02				<0.01		0.02
	Jasmimum abysinica	<0.01			0.02	<0.01					0.02
	Peponium vogelii	0.01			<0.01		<0.01		<0.01		0.02
	Toddalia asiatica		0.01		<0.01				<0.01		0.01
*	*Achyranthes aspera*				0.01	0.01					0.01
*	*Maesa lanceolata*						0.01				0.01
	Keetia gueinzii				0.01	<0.01			0.01		0.01
*	unidenified vine				<0.01		0.01			<0.01	0.01
	Callistemon citrinus	0.01									0.01
	chicken egg									0.01	0.01
	Citrullus sp., watermelon		0.01								0.01
	Smilax anceps				<0.01	<0.01	<0.01				0.01
	Vigna sp.				0.01	<0.01	<0.01				0.01
	Tabernaemontana usambarensis (ventricosa)				0.01		<0.01				0.01
	Calliandra gilberti					0.01					0.01
	Ritchiea albersii		0.01								0.01
	Justicia sp.					0.01					0.01
	Saccharum sp., sugar cane								0.01		0.01
	Scutia myrtina				0.01						0.01
*	*Cassipourea ruwensorensis*			<0.01	<0.01						0.01
	Ficus natalensis		0.01								0.01
*	*Momordica sp.*		0.01		<0.01						0.01
	Brunfelsia pauciflora	0.01									0.01

	Species/morphotype	Plant parts consumed									% of time feeding
		FL, FB	FR	LB	YL	YL & ML	ML	EX	ST & WD	UID	
	Acalypha neptunica		<0.01		<0.01	<0.01					<0.01
	Brassica sp., cabbage					<0.01					<0.01
*	*Cordia africana (abyssinica)*	<0.01									<0.01
	Ficus ovata				<0.01						<0.01
	Gloriosa superba				<0.01	<0.01	<0.01				<0.01
	Grass sp.					<0.01					<0.01
	Jasmimum pauciflorum			<0.01	<0.01	<0.01					<0.01
	Landolphia buchananii[a]									<0.01	<0.01
	Mangifera sp., mango		<0.01								<0.01
	Mayterius heterophylla				<0.01						<0.01
	Mondia whitei				<0.01		<0.01				<0.01
	Monodora myristica				<0.01						<0.01
	Oxyanthus speciosus		<0.01								<0.01
	Psychotria sp.					<0.01					<0.01
	Strombosia scheffleri	<0.01									<0.01
*	unidentified orchid	<0.01					<0.01				<0.01

Appendix IV. Diet composition by time and calories. Percentages are based on total feeding time. GN=124 female-days, TWS=123 female-days, GSC=124 female-days, Population=371 female-days. SD=standard deviation. I calculated values by first calculating daily values, then averaging over group and population. Categories were ordered by descending percentage of diet (kcal) of the population.

Food Categories	GN group				GSC group				TWS group				Population			
	Mean (by kcal)	SD (by kcal)	Mean (by time)	SD (by time)	Mean (by kcal)	SD (by kcal)	Mean (by time)	SD (by time)	Mean (by kcal)	SD (by kcal)	Mean (by time)	SD (by time)	Mean (by kcal)	SD (by kcal)	Mean (by time)	SD (by time)
% Fruit	57.79	27.34	42.76	23.02	59.87	26.49	40.02	19.74	51.09	24.32	35.23	19.38	56.24	26.28	39.34	20.72
% Young leaf	20.02	16.34	31.65	18.18	17.19	16.16	29.98	16.16	24.84	16.25	33.68	16.25	20.69	16.51	31.77	16.86
% Mature leaf	5.65	7.04	5.80	6.94	4.17	5.87	6.95	7.44	7.42	8.46	8.26	8.99	5.75	7.31	7.00	7.79
% Exudate	4.15	6.81	1.17	2.07	7.25	10.84	2.64	3.68	3.63	7.44	1.16	2.56	5.00	8.67	1.66	2.77
% Leaf bud	4.64	7.15	5.84	9.51	2.94	4.76	2.94	5.79	4.35	7.49	5.79	10.04	3.98	6.61	4.86	8.45
% Flower and bud	2.94	6.54	5.09	9.66	4.10	9.42	6.60	10.47	2.89	6.92	8.85	12.63	3.31	7.73	6.85	10.92
% Stem and wood	1.44	3.73	1.68	2.87	2.04	5.14	2.28	3.56	1.58	2.96	1.95	3.01	1.69	4.04	1.97	3.15
% Unidentified	2.23	5.53	1.09	2.46	0.80	3.05	0.51	1.43	1.08	3.68	0.53	1.43	1.37	4.26	0.71	1.77
% Human food	0.43	3.81	0.07	0.25	0.00	0.02	0.00	0.01	2.24	10.20	0.32	0.78	0.89	6.35	0.13	0.35
% Insect	0.60	1.03	3.85	5.22	1.30	1.69	7.96	6.77	0.75	1.06	2.88	3.22	0.88	1.33	4.90	5.07
% Mushroom	0.12	0.95	0.10	0.25	0.05	0.28	0.10	0.39	0.11	0.62	0.19	0.53	0.09	0.67	0.13	0.39
% Rock and dirt			0.91	2.64			0.02	0.06			1.17	3.99			0.70	2.23

Appendix V. RMTs showing grand mean of group daily diet intakes and group diet menus of important foods only. Polygons are composed of each groups' important foods (defined as >1% caloric contribution of calories consumed by group). Each polygon represents one group's diet of important foods. Labeled numbers represent the caloric contribution of important food items. The axes (x-, y- and implicit i-axis) are as follows: Protein x Lipid x Carbohydrate (relative percentages (by kcal)). Caloric value of structural fiber (NDF) in diet was calculated using group-specific digestion coefficients, see Methods. Polygons represent possible diets of important foods while solid, colored rectangles represent observed group diets (grand means (N=8 subjects per group, mean 15.46 female-days per subject)). A) represents GN group, b) represents GSC group and c) represents GSC group.